THE ESSENTIALS OF BIOLOGY

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BY

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INTRODUCTION

The intention of this book is to present a balanced account of the theoretical matter of animal biology. Botanical results are only noted in so far as they bear upon general biological science. All detail that is not illustrative of what may be called the principles of biology has been omitted, however attractive it may be. Doubtless the method of treatment leads to sins of omission, but it is hoped that these are not really important ones. There are vast masses of data in all departments of biology that have but slight relevance in general discussions, and the non-professional reader loses little by a careful selection of the essentials of the science. It must, however, be admitted that some parts of zoology present great difficulties to the reader who has not undergone the discipline of practical laboratory work on " animal types." I have tried to minimize these difficulties by giving a summary account of the forms of life looked at from the morphological standpoint, and this can easily be supplemented by study of the many excellent small books on special aspects of our science.

The present seems to be a very opportune time for making a survey of the main results of animal biology. The last forty years have been the period of a revolution in physics such as has no parallel, at any time, in biology. During this period the main lines of investigation in the biological sciences have been these : (1) biometry ; (2) the investigation of the cell and developing embryo, and (3) genetics and biochemistry. Biometrical methods, as they were elaborated by Weldon, Galton and Karl Pearson, have been so far perfected that they are now well ahead of the observational side of statistical biology, a line of research which is certain to be very greatly amplified in the future. We have, perhaps, now nearly come to a halt with respect to the pure morphology of the cell : further advances along that direction may well depend upon the improvement of methods of micro-dissection together with the development of

a technique of micro-chemistry. It is not too much to say that the results of genetical researches are now full of trivial detail, are rather dull and have little of far-reaching theoretical significance. Biochemistry, while not revolutionary, is full of interesting and stimulating materials: such are, for instance, the results of researches on vitamins and hormones and on rejuvenation. Without doubt much more in these directions may be expected in the near future.

The present phase in biology is to be regarded as essentially a critical-constructive one. The hypotheses of transformism, natural selection, Lamarckism, etc., are being "tried-out" and no one can say what is going to replace them. Not only the "Weismannism" of a former generation, but also the "Morganism" of to-day have proved unsatisfactory, although (of course) these investigations have left their marks on our science. Practical genetics is an old affair. In these lines of research a return to the old-fashioned natural history of the period of Darwin and Wallace is already indicated. Naturalists have been regarded as "scientists by courtesy," but much promise lies in the study of ecology—of organic habits in the wild. (Too much has been based on experimental work on the laboratory domestic animals!) The older, cruder materialism which emerged from the physiology of the medical schools has proved unsatisfactory when tested in the light of modern thermodynamical theory and we do not really know, in the least, what is going to replace it. A survey of biological science gives us certain indications that its growing-point, at present, is in biochemistry and that this growth of significant theoretical knowledge will be accelerated when it will have been possible to press new physical results into the service of biology.

It is very curious to notice how little the revolutionary, experimental methods of present-day physics have affected practical biology—and how much less speculative, mathematical physics has changed the attitude of speculative biology. Radioactive transformations seem to be affairs of inorganic chemistry. The annihilation of matter is said to go on in the interiors of hot stars and the creation of matter may, we are told, be proceeding in cold inter-stellar space, but there is no hint that these changes have any significance for the complex organic system of things. Electro-magnetic fields of force exist every-

where and may affect the grids of thermionic valves, but it has never been suspected that they may affect the much more delicate systems of nervous synapses. Cosmic radiation has easily been detected by gold-leaf electroscopes but, so far as we know, it has no significance for the organism. And so on. It has been suggested that life is a kind of affection of the (physically) dead, or dying, ashes of the substance of which stars are made! It is, of course, certain that this want of relevance, for biology, of the newer physical knowledge is only apparent and that the next revolutionary advance to be made by our science will be the application of these very strange physical results.

Even now, however, it is possible to apply to the study of biology the methods of thermodynamics and statistical mechanics. It is comforting to notice how, in the general confusion into which classical, theoretical physics has fallen, the classical concept of entropy has remained and has even been amplified. I have tried to suggest, in the following pages, what may be the importance of this conception even in the speculative biology of to-day.

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CHAPTER I

THE ORGANISM AS A NATURAL THING

1. *ON NATURAL THINGS*

By " natural things " we simply mean whatever can be investigated and described in a scientific way. Natural things are located in space and they endure, more or less, in time. They have forms and dimensions. They can be measured and weighed. In them energy-transformations occur, or they *are* energy-transformations. We can see, hear, smell, feel them and so on, either by our unaided sense organs or by means of the latter, reinforced by telescopes, microscopes, balances, spectroscopes, etc. In short, natural things are whatever become known to us in the data of sensation and are thereafter thought about.

They are the earth, the sun, moon, the planets and other cosmic bodies ; earth-features, that is the oceans and seas, continents, islands, etc. ; the water of the ocean, the atmosphere, sands, stones, rocks, minerals, etc. ; all chemical substances and mixtures of such ; all animate things and the things that are fabricated by animate things.

They are also whatever we cannot directly see, hear, smell, touch, etc., but whatever may be inferred by observations of some kind. Thus molecules, atoms, protons and electrons are natural things although we cannot see any of them and can only infer their objective existence by the observation of phenomena that are not molecules, atoms, etc. Forms of energy, that is, electric currents and charges, radiation, fields of force, etc., are also things in that they are measurable in space and time.

Thoughts in themselves, logical and mathematical relations, ideas, dreams, hallucinations, phantasms, etc., are not natural things in the sense adopted here.

1*a*. The Classes of Natural Things. These are (1) inanimate things, (2) organisms, and (3) artifacts. It is not easy to make rigid definitions that will include one of these classes of things and exclude the others, but these definitions are un-

necessary. We can easily *recognize* organisms and we can always be sure that a thing which we investigate is, or is not, alive. There are very few cases in the history of science where life was asserted of something that was not alive and in those cases the error was quickly detected. Artifacts can also be recognized, and here again it has not often happened that things fabricated by organisms have been mistaken for inanimate things and *vice versa*. Artifacts are lifeless things, but it is convenient to separate them from those other inanimate things that we consider here. In artifacts " life has gone over into its products."

2. *ON THE STATUS OF NATURAL THINGS*

Natural things have what we shall call " status " in relation to the passage of nature.

2*a*. The Passage of Nature. Nature, meaning all that we can observe and measure, continually changes and " passes." The great natural events, or changes, or phenomena, are the radiation of the stars and the partially-known changes in the interiors of the stars that maintain that radiation. The most familiar natural phenomenon that we know is the shining of the sun, the radiational energy of which is the cause of most of the things that happen on the earth. Less familiar are the great secular and cyclical changes in the earth itself, whereby mountain ranges are built up and become eroded away. These changes, in so far as they are not due to the sun's radiation, come from the original heat and other energy of the earth-interior and these came from the sun when the planet, earth, was formed. Thus the great universal phenomena are seen in the radiation of the stars, of which our sun is one.

The movements of the stars and planets are only physical changes in a restricted sense. These movements through space are impressive ones, but they do not involve the expenditure of energy—that is, no work is done in maintaining them. (This statement is not strictly true, as we may see by considering tidal friction, but nevertheless we may here neglect the very small energy-changes implied.)

Thus the sun and stars are to be regarded as reservoirs of energy. It will be seen from Section 89 that these energy-stores are being expended. The quantities of energy involved

are very great, so that cosmic bodies like the sun (and other stars) will certainly continue to radiate for millions of millions of years. Nevertheless, the changes that are involved in radiation are irreversible ones. It can be shown (see Section 89) that the continued emission of energy by the sun and stars is the result of the annihilation of their mass. Protons and electrons, which are the ultimate substance of the universe, may come together in such ways as to transform into radiation ; or they may come together to form atoms. The atoms of matter may continue to emit energy by undergoing radioactive disintegration, in the course of which changes their mass decreases. Moreover, all cosmic bodies which are hot radiate heat and become cool.

Radiation of any frequency tends to become universally distributed, travelling through cosmic space in all directions. Further, the radiation tends to degenerate inasmuch as its higher frequency tends always to become that lower frequency represented by heat of low temperature.

Thus the energy of the sun and stars continually degrades, in that it transforms into radiation, which becomes universally distributed and assumes the form of low-temperature heat. In the ultimate state of the universe all cosmic energy will take this form. This continued change is the passage of nature. (See further in Section 89.)

2*b*. THE ENERGETIC STATUS OF THINGS. Some natural things, such as the sun and stars, have *primary status* in that they represent physical causality. They radiate heat and other forms of energy and are the causes of physical events. Thus most of the changes of any kind that occur on the earth are the effects of the sun's radiation.

Things like the earth itself, its heated core, the chemically active materials in it and its envelopes are of *secondary energetic status*. Their energy, or physical causality, that is, their power of changing and setting up phenomena, are due to their original detachment from the sun—a thing of primary status.

Things like the nitrogen of the atmosphere, the cold materials of the rocks of the earth's crust, the substance of the moon, satellites in general, meteorites, cosmic dust, water, sands, etc., have (we may say in the meantime) *tertiary energetic status*. They are inert matter which no longer, of itself, is active in the

sense that it can enter into new chemical combinations, radiate heat, or undergo physical change, in general.

(But if we were to particularize we might, no doubt, make many energetic states of things, and it is possible that all matter may be undergoing very slow radioactive change, so that those things which we call inert may be physically active in an infinitesimal degree and over exceedingly long periods of time. If this is the case, the ultimate state of nature which passes is the dissolution of all things into chaotic, low-frequency radiation.)

2*c*. THE " MAKING OF THINGS." We may regard the universe as in the course of " being made." Things, like the substance of the interiors of the stars, are yet "unmade." They represent actual or potential causality and to some extent they may " become anything." They are enormous stores of energy which are dissipating themselves.

The older conception was that of a universe that had a fate, completely determined. The newer conception does not admit unique determination but rather the more or less probability of things happening. Thus while we may forecast the future of the sun, *to a great extent*, in that we can be sure that most of its energy simply radiates away into space, we cannot forecast what will be the fate of all of that part of the energy that falls on an earth which contains living organisms.

By the " making of things " we mean the assumptions of forms, materials, radiations, etc., that occur in the course of the passage of nature, that is, in the course of the degradation of the primary potentialities represented in the interiors of the stars.

2*d*. INANIMATE THINGS THAT ARE NOT YET COMPLETELY MADE. On the earth these are the heated earth-core, which continually gives off heat and contracts, thus producing surface inequalities, mountain ranges, running water, the ocean ; the heat received by the earth from the sun, which evaporates water and sets up ocean currents and winds ; all chemical substances that can still enter into combinations, etc. The physical potentialities of these things are not exhausted. In a large measure their fates can be predicted, but we shall see that these fates cannot absolutely be predicted and will not be so predicted with any increase in our knowledge of nature.

2*e*. INANIMATE THINGS THAT ARE COMPLETELY MADE. Such are (almost entirely) dark and cold stars, satellites, cosmic dust,

etc., chemical substances, like sands, no longer capable of themselves of entering into new combinations, the ultimate low-frequency radiation of the universe, etc. In respect of these things nature has passed.

3. *ON THE CHARACTERISTICS OF INANIMATE THINGS*

Inanimate things have a certain " individuality " in that they can be observed, measured and thought about by themselves. Thus the whole earth is a planet, having its mass and dimensions and its motions relatively to the sun, moon and stars : in these respects it is an individual thing. But we can find parts in the earth : thus it has a dense, central, metallic core ; a basaltic substratum, a siliceous lithosphere, a watery envelope, and an atmosphere. All these parts can be separately investigated. Also the lithosphere can be seen to be composed of igneous and sedimentary rocks of very many kinds. In the earth these various rocks are the parts of a structure and their characteristics can be stated in terms of their relations to other parts of the earth-structure. Thus the basaltic substratum underlies the lithosphere but rests on the metallic centrosphere : that may be considered as its main characteristic. But the basaltic substratum has this relation to the other earth-parts because of its mineral nature : it is lighter than the metallic centrosphere, or kernel, but it is heavier than the overlying lithosphere.

We can, however, isolate any part of the lithosphere and regard it as a thing quite apart from its relation to other things. Thus the Old Red Sandstone is a geological series of strata and its characteristics are that it was deposited after the Cambrian rocks were formed but before the Carboniferous ones were laid down. Yet a small piece of old Red Sandstone is a definite kind of rock quite apart from its place in the geological formations, and it has quite definite lithological characteristics. Again, this kind of rock is made up of grains of sand cemented together and each sand grain is a particle of silica. When we consider the form, the crystalline structure, the density and the chemical nature of a sand grain we think about it as a separate thing.

Clearly the individuality of inanimate things may be conferred upon them by our analysis of nature. Their characteristics may be their relation to other things. Thus an island is a piece of

land surrounded by water and a lake is a mass of water completely surrounded by land. The forms of the island and lake are not essential to their being islands or lakes and neither is the nature of the rocks of the island, nor the density of the water that is the lake.

The characteristics of other natural things may depend upon the processes by which they were formed and by the materials of which they are composed. Thus a river delta is made up of sands and muds laid down by the current when it enters the ocean. Its form is determined, to some extent, by the condition that the materials are borne in suspension in rapidly moving water and fall to the bottom when the current loses its velocity, but it is also determined by the coarseness, or fineness, of the particles and by their specific gravity. Again, a volcanic cone acquires its characteristic shape because of the way in which its materials are ejected into the air and then fall down, forming slopes with characteristic "angles of repose."

Thus islands, continents, capes, lakes, volcanoes, mountains, rivers, etc., are *amorphous-heterogeneous things*. They may have many forms and they may be composed of many kinds of materials without ceasing to be what they are. It is in their nature to have certain definite relations to other natural things: thus if the sea round about an island falls in level the island may cease to exist although its materials and form persist.

Natural things may be *formed and heterogeneous*. Thus the earth itself has definite spheroidal form though its materials are of many kinds, while the moon and sun have also forms that are characteristic though their materials are also heterogeneous and are not quite the same as the earth-materials. Water-worn pebbles in the bed of a river may have definite spheroidal form though they may be composed of many different kinds of rocks and minerals.

Very many kinds of inanimate things are characterized by their chemical composition. Calcium carbonate, for instance, may be an amorphous precipitate, or the limestone composing a fossil coral, or it may be globigerina ooze, or a crystal of Iceland spar. Regarded as the chemical substance, $CaCO_3$, the form of the thing that we see and handle and analyse does not matter: it is still $CaCO_3$ in all its forms. We say that it is *amorphous and homogeneous*, for it is essential to its being calcium carbonate that,

whatever it may look like, it is still the homogeneous chemical substance $CaCO_3$. Diamond, the deposit on the inside of a gas-retort and the substance of a black-lead pencil are all carbon.

Many kinds of inanimate things are characterized by their forms and their chemical compositions. Thus calcite is calcium carbonate that has crystallized in rhomboidal form. All crystals have both form and chemical composition, both essential to their nature. Crystals may have the same form but different chemical composition—if so they are not the same things. Crystals are usually *formed and homogeneous*.

Inanimate things may have characteristic forms that are not determined by their composition and which persist even though the materials of which they are composed do not persist. Thus a cyclonic storm is an eddy in the atmosphere and a whirlpool is an eddy in water. The form of the whirlpool may persist although the water of which it is composed changes from second to second. Such things are *material fluxes*.

4. *ON ORGANISMS AS NATURAL THINGS*

There is a modern " organic theory of nature " in which the term " organism " has been applied to things that are composed of parts and in which these parts have definite relationships to each other so that they make up complex things that have individualities.

Thus an atom is an " organism " in this sense, being composed of a system of electrons constituted in a certain way ;

A molecule is a definite arrangement, in space, of atoms ;

A colloidal particle is an orderly assemblage of molecules ; and so on.

But an atom has not always been the same thing. Before 1890 it was a perfectly hard, perfectly elastic, finite but indivisible particle ; J. J. Thomson's atom was a sphere of positive electricity in which negative electrons were embedded ; Bohr's atom was a system composed of a positively charged nucleus round which revolved satellite electrons in definite orbits. We may regard the atom as being constituted by protons that form a nucleus. There are " atmospheric " electrons outside the nucleus, but the inner electrons occupy whole orbits rather than revolve in orbits,

while the outer electrons are regarded as particles that revolve in orbits (but their motion in orbital paths cannot be traced).

Obviously an atom, in current physics, is a " model "—it is *constructed* by the human mind to explain the observable, measurable variations in the field of force that " surrounds " an atom (which really *is* the atom). It is something *that has been organized* rather than an organism. So also with concepts such as molecules and colloidal particles.

Thus a mob is unorganized, but when disciplined and commanded it may become a regiment of soldiers. Workers are organized into trade unions and so on.

In the organic theory of nature we deal with things *that are the results of organization*, that have been arranged and assembled. These things may not be alive (atoms, molecules, etc.) or they may be alive (communities, armies, legislatures, etc.). Organisms, which are things that we recognize as being alive, have this power of organization or arrangement.

And the definite parts and assemblages of parts, and motions of parts that we ascribe to the atom are different in different stages of our knowledge of nature because we attain greater power over nature and so observe phenomena that were unknown in the earlier stages. And as this control increases we explain new phenomena by means of new, hypothetical models.

Organisms we shall regard as things that are alive. Life is simply recognized by us, without any doubt at all, and without any necessary confusion with not-life. There may be difficulty in so *describing* a thing which is alive because inanimate things, artifacts and living things can only be scientifically described in terms of space and time measurements. All have shapes, dimensions, motions, colours, etc., and it does not seem possible, by employing space-time data alone, to make absolute distinctions, in verbal descriptions, between living and non-living things.

So far, then, as it appears to be possible organisms may be generally described as follows.

a. THE CHARACTERISTICS OF ORGANISMS.

i. *There are categories of organisms*. An individual organism is an example from a category, or kind (species, sub-species, race or variety) of organisms. Thus a single herring is an example of the species *Clupea harengus*.

The species, or category of organisms, contains, or includes,

a vast number of examples, and this number tends to become indefinitely great without limit.

There are very many categories of organisms and this number tends (in the course of the evolutionary career) also to become indefinitely great without limit.

Although all organisms can be arranged in categories (such as the species of the systematists) and although all the individuals of a category can be recognized as belonging to that category, yet all these individuals are, in some respects, different from each other.

ii. Each kind of organism has an essential "form." This form of body is characteristic and all the organisms contained in the species exhibit it, and it is not exhibited by the organisms contained in any other species. The form is so characteristic that the species to which an individual belongs may be recognized even when only a fragment of the body is seen. (These remarks apply to species that we know very well. There is often difficulty in recognizing the species of an organism, but this must be regarded as due to our insufficient knowledge, or inexperience of the species in question. The more intimately we know species of animals the more characteristic do their forms appear to be.)

iii. The "form" of an organism is a career. That is, an individual organism exhibits a passage from the embryonic phase, through juvenescent and adult phases, towards senescence and death. Its form is not the same in all these phases because it undergoes a process of development from an original, initial and undifferentiated phase in the ovum, or other beginning. Yet the form, or structure, of the ovum, embryo, larva, young, mature and senescent phases of the organism is always essential and characteristic. It can be recognized as that of the species and it may not be mistaken for any other species.

iv. Organisms grow by selecting and reassembling the materials of the medium in which they live. Crystals also grow by selecting materials from the medium (or mother-liquor) in which they are placed, but this is not the same kind of process as that of organic growth. The materials, or molecules, which compose the substance of a crystal are chemically similar to those which exist in the mother-liquor, whereas the materials of the body of an organism are not the same as the materials in its medium. For instance, the materials of the body of a green plant are water,

mineral salts, cellulose and other carbohydrates, proteins, fats, oils, waxes and resins, etc., whereas the materials that are taken into its body are water, mineral salts, carbonic acid and simple inorganic compounds of nitrogen. The elements of these food materials are the same as the elements of the bodily substances, but they are re-assembled after being absorbed into the body of the plant.

v. The body of an organism is a flux of materials. This is also the case in a whirlpool where the form of the thing endures although the materials (the water) that compose it are continually changing. But the material (water) which enters the whirlpool is of the same kind as that which is in the whirlpool and that which leaves it. The materials which enter the body of the organism—that is, its foodstuffs—are different from the materials of the tissues and from the materials (the excretions) that leave the body.

vi. Organisms reproduce. That means that the body of a mature animal or plant periodically dissociates into one part (which usually retains the normal and characteristic bodily form) and other parts (which have not that form). These other parts are the ova and spermatozoa. They have the powers of growth and differentiation, that is, they select and reassemble the materials of the media in which they live and they gradually assume the form that is characteristic of their parents. The numbers of organisms contained in any species becomes great *acceleratively*, the acceleration depending on the reproductive constants of the species.

vii. Organisms retard the process of energy-dissipation. Thus sunlight which falls on inanimate things is almost entirely dissipated into heat which then distributes itself throughout space. But sunlight which falls on the tissues of a green plant is utilized by the organism in bringing about the chemical combination of carbonic acid and water to form sugar and starch. Thus the available energy of the sunlight becomes accumulated (as potential chemical energy) in the tissues of the plant.

viii. The bodies of organisms are formed-heterogeneous things. That is, they have essential forms, like crystals, but they are composed of a great number of chemical substances.

ix. The substances of the bodies of organisms are relatively complex. The substances of inanimate things are relatively simple, that is, their molecules are composed of few atoms. The most

complex of inanimate things are the "organic" carbon-compounds and the silicates of which igneous rocks are composed and the molecules of these silicates may contain only some dozens of atoms. But the molecules of proteins in the bodies of animals and plants are composed of tens of thousands of atoms.

x. Some kinds of chemical compounds are present only in the bodies of organisms. Proteins, fats and carbohydrates are the typical chemical substances that compose the bodies of organisms and these substances do not exist among inanimate things. They can be found in artifacts, that is, they have been made by organisms. Proteins, fats and carbohydrates may now be regarded as having been synthesized by experimental chemists, but that means that they have been produced, or assembled by living organisms. It is immaterial to this description that the green plant synthesizes sugar automatically (and easily) while the chemist does so deliberately (and with difficulty).

5. *ON THE ORGANISM AND ITS ENVIRONMENT*

So far we have regarded organisms as natural things which we can detach from nature in general and study separately from all other natural things. This, however, is not true, though it has been a convenient (and necessary) step in our descriptions. Organisms cannot exist apart from the other natural things which surround them and exist contemporaneously with them. An organism is not a thing in the sense that a diamond, a physically dead planet, or a rock is a thing: it is "something happening." Since it is a flux of materials we must consider along with it all those other natural things with which it has traffic, or relations of any kind. If we were strictly to isolate an animal from its environment it would die in a short time—a very few minutes in the case of a mammal and a little longer in the case of some lower animals. Obviously a mammal must respire and respiration involves the environing oxygen of the atmosphere.

5*a*. THE PHYSICAL STATUS OF THE ORGANIC ENVIRONMENT. We have seen that in the passage of nature natural things become "made." It is easy to contemplate the complete making of a part of the universe, say the solar system. The time must come when the internal energy of the sun will be exhausted, or so nearly so that it will no longer emit radiation. By that time

the internal heat of the earth, and other planets, will have become completely dissipated. Oceans and atmospheres will become solid materials and the crusts of the planets will become rigid. Because of the immobility of these envelopes there will no longer be tides and so tidal friction will no longer affect the relative distances of the sun, planets and satellites and the periods of their revolutions and rotations. In that phase we may regard the solar system as having become stabilized, or made, for the energy received by it from the radiation of the stars may be neglected.

To an intelligent observer situated outside the solar system and able to measure the motions of the various bodies there would be absolute determination in those motions. (" Stability," it should be noted, does not involve the immobility of sun, planets and satellites : bodies in uniform motion will continue in those states, for no work is done by them in the absence of any resisting media.) From any one phase in the solar system, as thus made, any future or past phase could be predicted without error.

Such an environment could not permit of life, as we know it, or can imagine it, for it would be an environment in which all energy-transformations would have ceased. The temperature, for instance, would be that of cosmic space, and we have been able to observe the behaviour of living things (of very simple organic status) at temperatures only a few degrees higher than that of cosmic space. At such temperatures some primitive organisms, such as some seeds, or the spores of bacteria may continue to live during the periods throughout which the very low temperatures can be maintained. They do not function in any way, or we may regard their rate of functioning as proceeding " infinitely slowly." It is not merely because of the extreme " cold " that life is thus suspended—it is because energy-transformations between the organism and its environment have practically ceased.

The environing media of organisms are parts of the universe that are incompletely made. In these parts there is available energy that is undergoing dissipation : there is, for instance, radiation that is about to transform in some way or other, and there are chemical substances in such states that they can be oxidized, or combined with other substances so as to generate energy as heat, electrically, or in some other form. The environment in

which organisms can grow, reproduce, behave or otherwise function must be one in which energy in the available form is present and is undergoing dissipation.

5*b*. THE PHYSICAL STATUS OF ORGANISMS IN THE PASSAGE OF NATURE. An environment, in which there are organisms, is to some extent indeterminate : that is, it is impossible to predict what any future state will be, knowing only the present and past states. This indeterminism would exist even if our knowledge of such an environing physical system were quite complete. Let this be quite clear : in a physically dead, " made " solar system —one in which all energy were completely dissipated—there would be absolute determinism so that any future state could be precisely predicted from a knowledge of the masses, distances and motions of the various bodies in the system. But in a solar system such as our one is at the present time there cannot be absolute determinism, for the system contains organisms. The degree of indeterminism will depend on the degree to which the solar system is already made and on the powers of the organisms : the less the system is made (that is, the greater its available energy) and the more highly evolved the organisms are, the greater will be the degree of indeterminism.

Let man, in his scientific phase, be the organism that we consider. To prove our proposition it is necessary to show that there is " free-will " in man—that is, that he can *choose* between one action and another, or between acting and not-acting. He must be free to deliberate and choose, that is, the choice that he makes must not depend on what he has already done, or upon anything in his environment. Clearly we are not absolutely free in these ways—that is, we are, to some extent, *constrained* to act in this way or that. The constraints depend on the condition that our universe, or solar system, or environment, is partly made, and to the extent that it is made there is determinism. We have the intuition that we are free to choose between some alternatives and this intuition regulates our conduct as social organisms. Thus we praise or blame, punish or reward our fellow-creatures according to the ways in which they act socially. If we really believed that their actions were determined we should not praise, blame, punish or reward. But we actually do so and social systems are successfully built up accordingly. It is quite impossible to prove that our actions are always strictly determined

—indeed the problem of free-will has been regarded as a pseudo-problem and the amount of fruitless discussion that has been expended on it goes far to justify that way of looking at the question.

We take it, then, that, *to some extent*, man is free to do this, or that, or to do nothing at all.

And there is no result in biology that shows us that the evolutionary career is determinate. No biologist cares to predict what will be the future evolution of any species of organism. If human evolution is indeterminate so also is the power of man to act upon his environment.

Even with man's present powers the future phase of the solar system may be affected by him. Thus :

Tidal friction is slowly lengthening the day (or retarding the period of the earth's rotation on its axis). It is also increasing the distance between the earth and the moon. The latter body will very slowly recede from the earth ; will then begin to approach the earth again and will come so near that it will be broken up (by tidal disruption) into a system of small bodies such as those that compose the rings of Saturn.

But if man should choose to utilize tidal energy he will change the amount of tidal friction, will alter the whole tidal régime and will change, in some degree, the rates at which the above cosmic processes occur. True, the degree to which he could (with his present powers) influence the rate of tidal evolution is very small indeed—still, the theoretical possibility of his doing so exists, and whether he will do so or not, and to what extent his future evolution will enable him so to act, is, so far as we can see, indeterminate.

5*c*. The Nature of the Organic Environment. All the things and energies which an organism can utilize or which can affect it constitute its environment.

If there are things round about it upon which it cannot act, and which do not act upon it, these things are not in its environment, even if they are in more or less proximity to it. It is difficult to see, for instance, in what ways herrings in the Irish Sea can be affected by earthquakes in California or by the motions of Jupiter's satellites, yet these events and things occur and exist along with the herrings. They do not form part of the significant clupeid environment.

The motions of Jupiter's satellites and the apparent motions of the fixed stars are in the environment of man, for he can utilize these motions. He may find his longitude at sea by observations of the occultations of the Jovian satellites and he finds the moment of midnight by observing the transit of a fixed star. Even when man observes, but does not utilize some astronomical observation he *acts upon* the cosmic bodies that he observes—for the radiations from these stars *are* really the stars : the latter are wherever they act. And when the astronomer diverts stellar radiation into a spectroscope or camera, or when he adjusts telescopes, etc., as to cause that radiation to enter instruments, he acts upon it with his organs of sense and muscle.

Whatever, therefore, an organism acts upon, or utilizes, or avoids, or is affected by, is in its environment. And according to its status in the evolutionary career—that is, according to its power of acting upon natural things that are not already made, the environment of an organism is the more or less extensive. And things that are in the environment of one organism may not be in the environment of another one.

6. *ON ARTIFACTS*

Artifacts are natural things that would not exist apart from the existence of organisms. They are such as we see them, because their materials have come together by reason of the activities of organisms ; or they are things that have been segregated from other inanimate things ; or have been modified or shaped ; or have been manufactured consciously or unconsciously by organisms. Examples are coal, peat, vegetable mould, globigerina ooze, limestones, coral reefs, fossils, chalk, worm-reefs, the nests, burrows, hives, houses and other shelters of animals, human habitations, cities, roads, harbours, ships and other vehicles, weapons, tools, machines, synthetic chemical substances, fabrics, etc.

They are lifeless things, but they obviously belong to a different category of natural things from those that we have called "inanimate."

Artifacts are not all of the same kind. Organic remains, such as coal, oil found in shale-beds, shelly gravel, adipocere, etc., are the chemically altered tissues of the dead bodies of plants or

animals. Generally these tissues undergo complete disintegration so that their substances are decomposed, either purely chemically, or by the activities of bacteria, into the stable substances, carbonic acid, water, simple nitrogenous compounds, sulphates, and phosphates, etc. But occasionally the organic tissues may be partially preserved, after death, with the results that artifacts such as we have mentioned may be formed.

Fossils are artifacts of a different kind. In them the chemical elements of the original organic body do not (normally) exist. Thus coal contains some of the carbon that was present in the cellulose of the plants that gave rise to it, but tree-trunks that may be found in coal-beds, or elsewhere, as fossils may not contain carbon. In typical fossils the tissues become mineralized, that is, the carbonaceous materials, or the calcareous ones, become replaced by other materials (usually lime or silica). Yet the replacement occurs in such a way that the formation of the tissues may be preserved. The structure of the latter may be the same in the fossil as it was in the living organism, though the actual materials that manifest this structure may be entirely different.

What we generally call an artifact is an inanimate thing, or a number of such, that have been modified in some ways *so as to subserve a purpose*. Thus many marine worms pick up sand grains and cement these together to form tubes in which they live ; a hermit crab chooses an empty gastropod shell and backs into this so that it inhabits it ; a fox may find a natural hole in the earth and there enlarge it to form a home, or a bird may collect and arrange twigs of wood to make a nest. All these things are artifacts in the ways in which they are used. The stone that is used by a thrush in order to crack snail-shells upon is also (though in a rather different way) an artifact.

Typical artifacts are houses, clothing, tools, etc., made and utilized by man. In these cases the choice of the natural things is conscious and deliberate (though in lower animals the choice may be instinctive and perhaps not even conscious). The natural things are modified and shaped and this too may be instinctive in the lower animals but deliberated, or even *designed*, in the case of man. Thus in artifacts, the notion of purpose may be implicit : the thing, whatever it may be, has had, or has usefulness of some kind. It is employed to do something and it may even be

imagined, before it was actually made, with a purpose in contemplation. It is in this way that man makes machines.

In all artifacts some external agency has been operative. Natural, inanimate things may have structure, but this structure is due to tendencies inherent in the things themselves. The earth, as a planet, has structure in that it consists of a metallic kernel, a basaltic substratum, a lithosphere which is broken up into continents, a watery envelope and an atmosphere. This structure is the consequence of the original state of the earth: when it was detached from the parent sun it was a mass of incandescent gas that had a motion of rotation. Gravitation, the loss of heat by radiation and the physical and chemical properties of the original earth-materials modified the latter. The structure of the earth is therefore due to intrinsic agencies that operated, *of themselves*, and which had tendency. The tendency was that which is in the passage of nature and expressed the movement towards ultimate stability.

In all artifacts we can trace the operation of agencies external to the inanimate things that were utilized, or segregated, or fabricated, and these agencies are the life-impulses of organisms.

Man tends more and more to form about himself an environment of artifacts. Civilizations, cities, ships, railways, houses, machines, tools, elaborated clothing, cultivated foods, synthetic chemical substances, etc., now form much the more significant parts of his environment. Before man these things did not exist and they are truly parts of nature made, not in the passage of nature, but by man himself.

CHAPTER II

ORGANIC STRUCTURE

I. CHEMICAL

Organisms, still considered as natural things, have structure. They have definite, specifiable shapes and dimensions ; they have bodies, limbs, etc., that have definite proportions to each other ; they have colours, consistencies, etc.—that is, they have external morphology. They are composed of parts that become visible upon dissection and they have definite and specifiable chemical constitutions.

It is quite impossible to consider this structure apart from considering organic behaviour and functioning and (either patently or surreptitiously) we introduce the latter notions into descriptions of morphology and chemical structure. However, it will be convenient for exposition to regard organisms, in this place, from a static, rather than from a dynamic point of view.

From the morphological standpoint organisms exhibit *patterns* of structure and the number of such patterns (specific forms) tends to be indefinitely great. Each pattern is exemplified in many individuals and the numbers of individual exemplars also tend to be indefinitely great.

From the chemical standpoint there are also patterns of structure : in all organisms the characteristic substances of the bodies are proteins, carbohydrates and fats, but different categories of organisms exhibit different kinds of these general materials. Plants have much cellulose in their bodies and may have silica as the material of their skeletal parts ; some animals have siliceous skeletons while most have calcareous ones ; and so on. The number of organic chemical patterns is far more limited than the number of morphological ones.

7. ON THE ULTIMATE CHEMICAL STRUCTURE OF ORGANISMS

7a. The Ultimate Chemistry of Inorganic Things. A small part of the earth is known directly—this part includes the rocky crust to a few miles deep; the watery envelope, or ocean, and the gaseous envelope, or atmosphere. The deep interior of the earth is indirectly known.

The outer envelopes of the sun and the stars and the materials of some nebulæ are directly known in that it is possible to deduce the chemical materials from the nature of the emitted light-radiation. The chemical structure of some meteoritic bodies is directly known.

It is possible to infer the chemical structure of those parts of the universe that are not directly accessible to observation. With such reservations it may be stated that the ordinary matter of the universe is constituted by about 100 different kinds of chemically elementary substances.

The crust of the solid earth. The most frequently occurring chemical elements and their percentages of the earth's crust are oxygen 50 per cent., silicon 26, aluminium 7, iron 4, calcium 3, magnesium 2, sodium 2, potassium 2, hydrogen 1, titanium 0·5, carbon 0·18, chlorine 0·2, bromine 0·2, phosphorus 0·11, sulphur 0·11, barium 0·08, manganese 0·08, strontium 0·02, nitrogen 0·03, fluorine 0·1, all other elements 0·5 per cent. Thus about 90 per cent. of the directly known materials of the solid crust of the earth consists of the five elements oxygen, silicon, aluminium, iron and calcium.

The watery envelope. This consists of oxygen and hydrogen, in the form of water, and contains, in solution, about 3·5 per cent. of other elements, mainly sodium and chlorine. There are measurable, or unmeasurable, minute quantities (say per 10 litres) of nearly all the other known elements.

The gaseous envelope. This consists of about 79 per cent. of nitrogen, 20 per cent. of oxygen, water vapour, carbon dioxide, oxides of nitrogen, argon, helium, hydrogen, etc.

7b. The Ultimate Chemistry of Organisms. There are very few complete analyses of the bodies of animals or plants. The following, however, is the ultimate composition of the body of a man:

Oxygen 65 per cent., carbon 18·25, hydrogen 10, nitrogen 2·5, calcium 1·5, phosphorus 0·8, potassium 0·27, sodium 0·26, chlorine 0·25, sulphur 0·24, magnesium 0·04, iron 0·02, all other elements 0·87 per cent. This may be taken to represent approximately the ultimate chemical composition of the body of a vertebrate animal. Such animals differ chemically in respect of (1) the percentage of water, (2) that of the mineral part of the skeleton and (3) the relative mass of horny (proteid) matter.

Other animals differ from vertebrates mainly with respect to the nature of the chemical substances that compose the skeleton : these may be (1) lime and magnesia carbonates and phosphates ; silica ; strontium carbonate or phosphate. The percentages of water in the body also differ, being about 90–95 per cent. (in the cases of some jelly-fishes) to about 50–60 per cent. (in vertebrates, etc.).

Thus our knowledge of the chemistry of inorganic and organic things, earthly and celestial (in the cases of inorganic things, of course), shows that :

No chemical element occurs exclusively in the bodies of organisms.

7c. WATER AS A NATURAL THING. Water exists mainly in the ocean and atmosphere. It is a constituent of all inorganic (mineral) materials, even of molten magma or of volcanic lava. It is present to the extent of about 50 per cent. or more, in general, in the bodies of animals and plants. It is an almost universal solvent, so that almost all elements occur, in some form, in sea water. Most chemical substances combine with it when they crystallize. Most substances that dissolve in it dissociate into sub-compounds that are chemically more reactive. A very great number of chemical reactions only proceed in the presence of water.

All the characteristic substances found in the bodies of plants and animals are only organically significant because they contain half or more of their weight of water.

Water is, therefore, a general medium in which both organic and inorganic processes occur. Its presence is characteristic alike of the organic and inorganic physico-chemical systems that we know. We may therefore assume its general occurrence and consider the characteristic chemical elements apart from it that are present in organic and inorganic things.

7d. THE CHARACTERISTIC ELEMENTS IN ORGANIC AND INORGANIC THINGS. Simplifying the matter by regarding water as the immediate medium in which both organic and inorganic chemical substances react we find these elements to be those characteristic of the two great classes of natural things :

Inanimate things : Oxygen, silicon, aluminium, iron, calcium.

Organisms : Carbon, nitrogen, hydrogen, oxygen.

8. *ON THE CHEMICAL COMPOUNDS THAT COMPOSE THE BODIES OF ORGANISMS*

First we consider the chemical compounds that make up inorganic things. A cursory survey of the field of inorganic chemistry shows very different kinds of chemical categories than we find in the bodies of organisms.

8a. INORGANIC CHEMICAL CATEGORIES. *First*, then, the elementary substances :

Metals—(iron, nickel, copper, etc.) inferred to be present in the heated centrosphere, or " kernel " of the earth. *Noble metals* (gold, platinum, etc.) present in small quantities in the rocky crust ;

Non-metals—Sulphur, hydrogen, etc., present in volcanic emanations ; oxygen, nitrogen, argon, helium, etc., present in the atmosphere.

Second. There are the characteristic mineral substances of the earth's crust :

Silica, silicates of aluminium and the alkaline and earthy metals ;

Carbonates (of lime, magnesia, etc.) ; oxides (such as those of iron) ; sulphides (iron pyrites, for example) ; phosphates (such as apatite) and so on ;

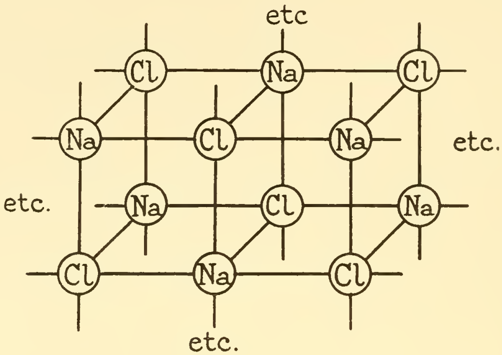
The water of the ocean, of ice and snow and of lakes and rivers ; the water and carbon dioxide of the atmosphere and so on.

Chemically these categories of natural things are structurally simple ; thus

$$\text{Water—}H - O - H$$
$$\text{Carbon dioxide—}O = C = O$$
$$\text{Silica—}O = Si = O$$

But this simplicity, as it is represented above, is fictitious :

the formulæ represent individual molecules and it is not such that exist in the rocks and minerals. Thus rock-salt (sodium chloride), as a molecule, is simply Na — Cl, but in rock-salt crystals we have really a solid "lattice":



And in crystals (out of which most mineral substances are constituted) this lattice-work in three dimensions may be exceedingly complex. Nevertheless, the molecular weights (that is the weights relatively to the molecule of hydrogen = 2), when it is possible to infer these, have the relatively low values of tens to hundreds of units in the cases of inorganic substances.

8*b*. Organic Chemical Categories. Here the molecular weights have the values of thousands to hundreds of thousands of units.

Characteristic organic chemical substances are proteins, carbohydrates and fats: each of these is really a category, so that there are very great (though finite) numbers of different proteins, etc.

Proteins. These are chemical substances, of which the molecules may be regarded as being built up as follows:—

The "building-stones" are *amino-acids*;
Amino-acids are built up into *polypeptides*;
Polypeptides are finally built up into proteins.

An amino-acid may be *arginine*, which is

$$NH = \overset{\displaystyle NH_2 \atop |}{C} - NH - CH_2 - CH_2 - CH_2 - CH(NH_2)COOH.$$

And the characters of an amino-acid, from our present point of view, are the presence of the groups of atoms—

$$-NH_2 \text{ and } -COOH.$$

Amino-acids link together by the "condensation" of these groups thus

$$\underset{\text{Glycine}}{NH_2 - CH_2 -} \underset{\underset{OH_2}{\downarrow}}{\boxed{COOH + NH_2}} \underset{\text{Alanine}}{- CH - CH_3 - COOH.}$$

The parts of the two molecules enclosed in the dotted square combine, at the same time eliminating the elements of water, $\longrightarrow OH_2$, and the result is a *dipeptide*. The latter has, at its ends, the characteristic protein linking-groups, NH_2 and $COOH$, so that it can still condense with one or more amino-acid molecules, to form a *tri-* or *poly*-peptide. Thus we have the next higher building stones.

Polypeptides link together (how exactly we do not know) to form protein molecules. Thus

$$\text{etc.}-\left\{\begin{array}{l}\text{Arginine}\\ \text{Serine}\\ \text{Arginine}\end{array}\right\}-\left\{\begin{array}{l}\text{Arginine}\\ \text{Protine}\\ \text{Arginine}\end{array}\right\}-\text{etc.}$$

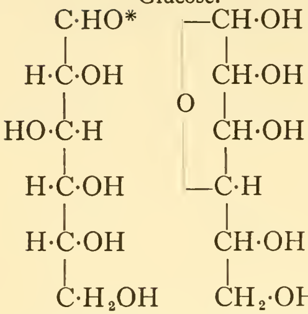
The primary building stones, or amino-acids, may themselves be very complex. Thus tryptophan is

$$NH\left\langle\begin{array}{c}CH\\ \\ C_6H_4\end{array}\right\rangle C - CH_2 - CH(NH_2)COOH.$$

And long chains, rings and perhaps spirals of linked amino-acids form the polypeptides. Obviously the protein molecule is a highly complex structure and the above suggestions only faintly indicate the degree of such complexity. Characteristic of the proteins are (relatively to the carbohydrates and fats) the presence of nitrogen (and sulphur) in the amino-acid building stones. We easily see how huge molecular weights can be attained.

Carbohydrates are chains of carbon-atoms $-\overset{|}{\underset{|}{C}}-$ which read as though they contain characteristic groups in certain positions in the chains, although recent research shows that they have an oxide ring structure.

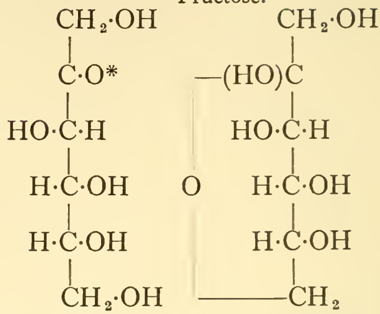
Glucose.



Older Formula
* Aldehyde Group

Oxide Ring
Formula

Fructose.



Older Formula
* Ketone Group

Oxide Ring
Formula

This is the general type of structure, varied and extended in almost innumerable ways. Among the carbohydrates are all the sugars, starches, glycogens, celluloses, etc.

Fats. Typical oils and fats are *glycerides.* Glycerol (or glycerine) is an alcohol (that is, a carbon chain substance with three of the hydroxyl groups, —OH) : it is

$$\begin{array}{ccccc} CH_2 & - & CH & - & CH_2 \\ | & & | & & | \\ OH & & OH & & OH \end{array}$$

" Fatty acids " are also long carbon chains which have the terminal group —COOH. Thus stearic acid is

$$CH_3.[CH_2]_{16}.COOH$$

Such an acid can attach itself to an — OH group in an alcohol, by eliminating OH_3 from the attaching radicals, — OH (in the alcohol) and —COOH (in the acid). Thus tristearin (of mutton fat) is

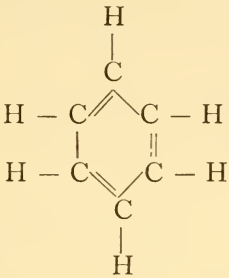
$$\begin{array}{l} CH_2 - O - CO - [CH_2]_{16} - CH_2 - CH_3 \\ | \\ CH_2 - O - CO - [CH_2]_{16} - CH_2 - CH_3 \\ | \\ CH_2 - O - CO - [CH_2]_{16} - CH_2 - CH_3 \end{array}$$

Isomerism and stereoisomerism. (1) Consider the carbon chain $CH_3 - CH_2 - CH_2 - CH_2 - CH_3$; and transpose the C's, with their attached H's thus—

$$\begin{array}{l} CH_3 \\ | \\ CH - CH_2 - CH_3 \\ | \\ CH_3 \end{array} ; \text{ and again } \begin{array}{ccccc} & & CH_3 & & \\ & & | & & \\ CH_3 & - & C & - & CH_3 \\ & & | & & \\ & & CH_3 & & \end{array}$$

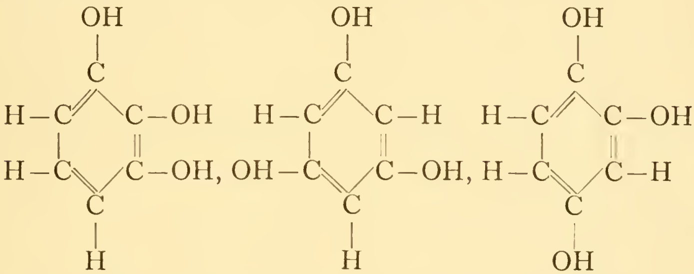
These three substances are all C_5H_{12}, but they are all different in chemical properties.

(2) Consider the "carbon-ring"



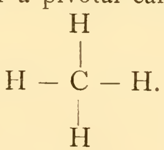
(which is benzene)

and suppose three of the $-H$'s replaced by $-OH$'s: there are three different substances formed in this way. Thus

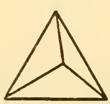


although each contains the same numbers of $-H$'s and $-OH$'s attached to the carbon ring.

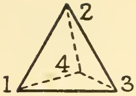
(3) Finally, consider a pivotal carbon atom, with its attached atoms or groups, say



In 3-dimensional space the carbon atom is situated in the centre of a tetrahedron,



and the attached atoms, or groups, are placed at the solid angles of the tetrahedron. If there are, say, four different attached groups, 1, 2, 3, 4, then we might see these (when we look at one face of the tetrahedron) thus

 (the fourth group being on the solid angle behind)

or thus 

and the two substances thus formed would not be, chemically and physically, the same.

These are instances of isomerism. Two substances might have exactly the same numbers and kinds of atoms, but they will differ if the distribution in space of the atoms is different. And so many rearrangements of the atoms and groups of a protein or carbohydrate are possible that billions of different substances formed from the same numbers and kinds of atoms are possible.

Other organic chemical substances. The above are the " foundation " categories of the chemical substances found in the bodies of plants and animals. There are many others. Proteins, carbohydrates, etc., may " conjugate," or join up in many ways. Inorganic chemical substances, sulphur, phosphoric acid, etc., may become incorporated in the carbon chains, rings, etc., and so on.

The organic " keystones " of chemical structure are carbon chains or rings, or nitrogen nuclei (see Section 73*a*). These two elements, C and N, have such extraordinary " pivotal " rôles, and the existence of isomeric arrangements is so fruitful of results, that the number of possible organic compounds, that is, those pivoted on binding C and N atoms, must be incredibly great. *But it is finite.*

And so very great is the power, or facility, of the carbon atom for building up complex chemical structures that huge molecules are formed. Some proteins may consist of tens or hundreds of thousands of atoms and have weights, relatively to the hydrogen-molecule, of hundreds of thousands. There is nothing like this in inorganic chemical substances.

8*c*. THE CHEMISTRY OF ARTIFACTS. Chemically artifacts " may be anything." They are things made consciously or unconsciously by man and other organisms and their chemical nature expresses purpose or tendency of some kind :

The metallic alloys of stainless steel—because that does not rust ;

Concrete and brick—clayey and cementing substances resisting crushing stresses;
Gold and platinum ornaments—partially because these metals do not tarnish;
Spider silk—fine and strong protein filaments capable of making traps;
Urea—a residue resulting from a metabolic tendency or a synthetic chemical substance. All such are obviously artifacts;
and so on.

II. ORGANIC STRUCTURE: MORPHOLOGICAL

A very great number of organisms, collected at random, can easily be arranged in categories, which we may here call *species* (but see Section 77). These categories are such that all the organisms in any one of them resemble each other much more closely than they resemble the organisms in any one of the other categories.

So that, given a great deal of experience, a systematist can generally refer any organism, collected at random, to its natural category. (That is, in respect of some large group of species well-known to the systematist, for organic nature is so rich in forms that it is not possible for anyone to acquire such an intimate knowledge of *all* forms of life.) This recognition of the specific position of any organism is based on inspection, simply, or assisted by the microscope, or supplemented by dissection: chemical structure, or morphology, is studied experimentally.

Groups of categories, that is, genera, families, classes and phyla of organisms, can be constructed (see Section 77). All the species in any genus resemble each other more closely than they resemble the species in any other genus. So also with the genera that can be grouped into a family, the families that are grouped into orders, and so on.

The species (or some other more elementary category (see Section 77*a*) is a natural category of organisms. Other and more general categories are logical constructions. The individuals grouped into a species are actually and always dissimilar, in detail, to each other, but here we neglect this individual variability. Because of individual variability, and of transformism, the number of organic forms is indefinitely great.

9. *ON UNICELLULAR AND MULTICELLULAR ORGANISMS*

The primary grouping of all organisms, whether plant or animal ones, is into such as have a body constituted by a single organic *cell* (see Section 9*a*) and such as have a body constituted by a number (usually a very large number) of organic cells. The unicellular organism, in general, is called a *protist* ; or a *protozoan*, if it is regarded as an animal, and a *protophyte*, if it is regarded as a plant.

There is not a rigid distinction between unicellular and multicellular organisms. Usually the above definition—one or many cells in the body—holds good, but sometimes the body of a protist is constituted by a small number of cells. Where this is the case the cells are to be regarded as forming a *colony* of similar protists, for they are not differentiated except in that some of them may reproduce while the others do not but simply exercise ordinary organic functions.

Protists are always relatively minute in size, varying in diameter from a few thousandth-parts of a millimetre to about one or a few millimetres. That is, there is a limit of size to which a protist may grow—why an unitary piece of organized matter can only attain a very small magnitude is a curious and unsolved problem.

The diversity in outer form and habits, and of internal bodily structure is very great. Thus a man, a fish, an insect, a cuttlefish and a sponge are remarkably different animals in every respect. There are many hundreds of thousands of *kinds* of plants and animals and the structural differences between these particular kinds of organisms include a bewildering mass of detail the description of which requires a large library, containing the transactions of most of the learned societies of the world. But most of this detail is unessential for the purpose of this book (though all of it may be necessary in the construction of a rational classification of organisms). From our point of view it is sufficient to survey the animal kingdom broadly. We can readily make a relatively small number of principal types of animals, each type being characterized by its general bodily structure and mode of life. In the series of types considered below the rational classification of animals—that arrangement which seeks to present a summary of blood-relationships, lines of descent, or evolutionary history, will not be strictly followed. It will present, rather, a

conspectus of animal bodily forms sufficient for a broad survey of the essential data of biology.

9*a*. THE ORGANIC CELL. This is either, in itself, a living animal or it is the unit, or element, of which the body of a living animal is made up. A Protist is usually a single organic cell. The red and white blood corpuscles, or other isolated units in the body of a multicellular animal, are organic cells. So are the elements into which microscopical analysis can decompose the tissues of all multicellular organisms.

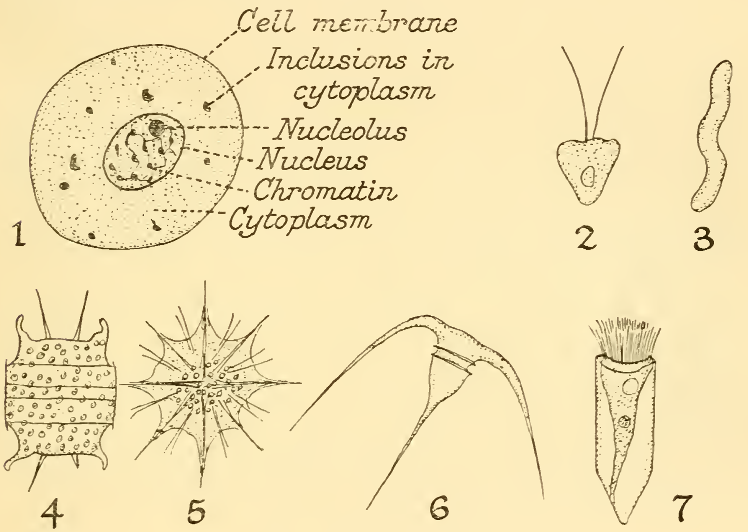


FIG. 1.—ORGANIC CELLS.

1, Diagram of a cell; 2, the Zoospore of an algal seaweed; 3, a Spirillum (Bacteria); 4, a Diatom; 5, a Radiolarian; 6, a Dinoflagellate; 7, a Ciliate (5, 6, 7 are Protozoa; 4 is a Protophyte).

Typically the cell is spherical in shape. It is bounded by a cell-membrane which may form a relatively thick wall. In the typical cell there is always a smaller roughly spherical body called the nucleus. The substance of the cell (outside the nucleus) is called *cytoplasm*: this we may regard as a chemically heterogeneous substance of which the constituents are water, mineral salts, proteins, carbohydrates, fats, lipoids, phosphatides, etc. In the cytoplasm there are usually inclusions, such as the chlorophyll plastids of the cells of a green plant. In the nucleus is a ground substance much the same as the cytoplasm but contain-

ing, as inclusions, the highly characteristic chromatin bodies. The above are the general characters of an *undifferentiated cell.*

9*b*. THE PROTIST BODY. Such may also be the general characters of the unicellular organism, or Protist. But such general characters are modified in detail so that there are multitudinous forms of Protists, defined by variations in the internal and external skeletal parts ; by differences in the size, form, etc., of the nuclei ; by differences in the numbers and natures of the cell inclusions, etc. These various forms of the Protist body can be arranged into specific categories just as in the cases of the multicellular organisms. The *Bacteria* are to be regarded as Protists, but here morphological categories cannot be made—partly because of the very minute sizes of the organisms, and perhaps because the specific categories may be based on the physiologies of the organisms. In practice categories of Bacteria are recognized by the activities of the organisms in acting chemically on the nutrient substances in their environments.

The Ultra-microscopic organisms. The existence of these is inferred. They are too small to be seen in the sense that an ordinary Diatom, say, is seen. Their presence can be detected microscopically but not their forms. There is a limit to the size of particles that can be seen, even in the perfect microscope, and this limit depends on the relative dimensions of light-waves and those of the particles envisaged. The conception of definite morphology therefore fails in these cases.

10. *THE MULTICELLULAR ORGANISM*

The bodies of the multicellular plants and animals are complexes of cells ; the cells are differentiated into kinds and the units of each kind are *tissue-elements.* Thus there are bone-cells, muscle-cells, nerve-cells, gland-cells, connective-tissue-cells, etc. Tissue-elements are compacted together into tissues and tissues have tectonic arrangements as organs. Thus organs are—skeleton shell, muscle-systems, sense-organs, etc. (see further in Section 12).

10*a*. SYMMETRY OF PARTS. The higher multicellular organism has parts which are more or less repetitional in structure, each part containing all or many of the organs that are also in other

parts. In a general way we may say that the animal body is *segmental*, each segment being more or less similar in structure to all the others. *In a rough sort of way* we distinguish these kinds of symmetry—that is, the various arrangements of segments :

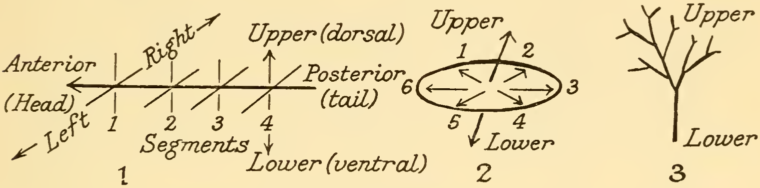


FIG. 2.—PRINCIPAL TYPES OF SYMMETRY OF BODILY SEGMENTS.

1. Triple animal symmetry (a fish) : There is differentiation in the anterior-posterior axis, between upper and lower (dorsal and ventral) parts and between the right and left sides. 2. Radial symmetry (a starfish) : There are upper and lower parts and parts are arranged radially about an upper-lower axis. 3. Racemose symmetry (hydrozoon or polyzoon) : The " body " (which is to be regarded as a " colony " of attached organisms) branches. The segments (or " individuals " of the colony) may have, each of them, radial, or bilateral (right and left) symmetry.

The segments are obvious or partially concealed parts of the animal body that are all more or less alike. The polyps, or zooids of a Hydrozoon, or Coral, we regard here as segments. So are the " arms " of a Starfish, the " joints " of an Earthworm or Tapeworm, the imperfectly differentiated " joints " in the body of a lobster, etc. The segmentation is never quite complete in the sense that all the segments are quite alike. The symmetry, also, may be confused and may partake of various types.

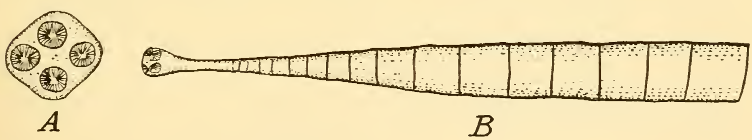


FIG. 3.

A. Head, or Scolex, of a Tapeworm (or Cestode). B. The anterior part of the same. Here the segments (proglottides) of the worm are very nearly all alike, developing in degree of sexual maturity from anterior to posterior. A detached segment is capable of independent existence. The Scolex shows radial symmetry.

10*b*. INTEGRATION OF PARTS. In no case have we, in the animal kingdom, exact repetition of similar parts, or segments. The latter always differentiate in form and exercise different functions, to some extent. Thus the diversity in the Cestode, as illustrated above.

We now form the conceptions of *Orders of Individuality and successive integrations.*

(*a*) *Individuals of the First Order.* The Protists (cells), unicellular organisms.

(*i*) *The First Integration.* Protists (cells) coalesce to form the simple, unisegmental body—such as that of a *Hydra*, giving—

(*b*) *Individuals of the Second Order* such as the Hydra, or sea-anemone. Multicellular and plurisegmental.

(*ii*) *The Second Integration.* Segments coalesce to form the pluri-segmental body—such as the siphonophone, vertebrate, etc., giving

(*c*) *Individuals of the Third Order.* All the higher animals. Multicellular and plurisegmental.

It is not altogether fanciful to see in the animal communities (the gregarious herd, the insect hive, the human society) a fourth order of individuality. A third integration has been effected by instinctive and intelligent activities, while in the human society the individuals integrate by traditions, laws, inhibitions, taboos, etc. In the insect communities there are structurally differentiated castles. In human societies castes have a basis in tradition. In these higher integrations behaviour is the main factor.

11. *ON TYPES OF ANIMAL STRUCTURE*

We attempt here to reduce the diversity of animal forms to a few general types. Detail is neglected and the morphology is idealized—to some extent.

11*a*. The Unicellular Type. The animal is either (and typically) a single organic cell, or a loosely compacted colony of cells that are alike in most respects (see Fig. 1).

11*b*. The Sponge Type. The sponge body may not have any essential and definite shape. It has rough upper and lower symmetry in that it is fixed to some support, such as a stone on the sea bottom. In its most simple form it is a sac. At the upper part of the sac there is, typically, a large opening, or osculum. Everywhere else there are pores in the wall of the sac. The pores lead into canal-systems and water, entering the latter by the pores, leaves the sponge body by the osculum, or oscula. The canals are mostly lined by a layer of " collar-cells " and the

whole sponge is essentially a congeries, or " colony," of such collar-cells. Apart from specialized reproductive cells and a supporting system of spicules, or fibres, there are no true tissues.

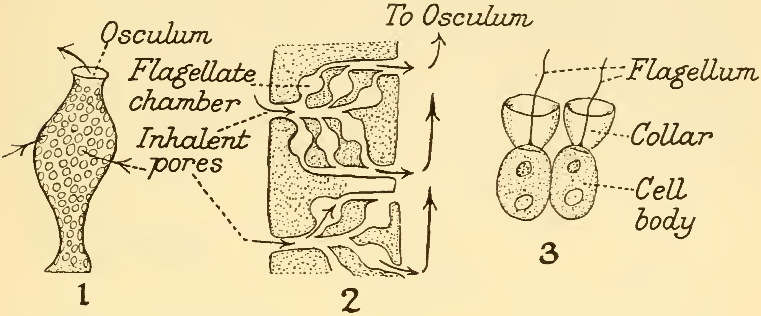


FIG. 4.

1, A very simple sponge; 2, diagrammatic section of the wall of such a simple sac-like sponge; 3, two of the characteristic, sponge " Collar-cells."

11*c*. THE HYDRA TYPE. Here we may have solitary individuals that are fixed to the stones, weeds, etc., in fresh or marine waters (*Hydra*, Sea-Anemones), or solitary, pelagic (drifting) forms (Medusæ or " Jelly-fish), or colonies of individuals having no particular arrangements. The structure is as follows:

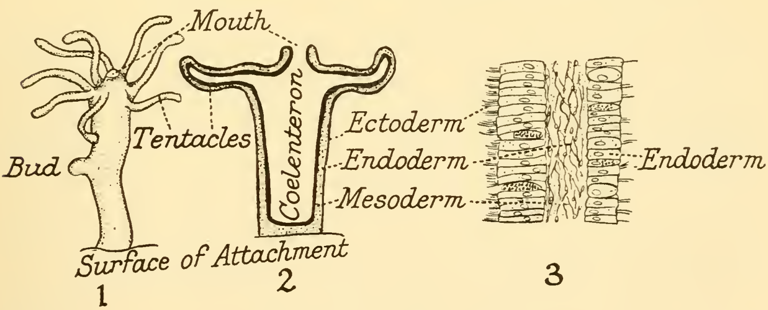


FIG. 5.—THE HYDRA TYPE.

Essential structure of the solitary forms referred to above, and of the Zooids, or segmental units of the Racemose type referred to below.

1, A *Hydra*; 2, diagrammatic section through one of such Zooids, or units; 3, section through the wall of a Hydra—this represents also the essential structure of the wall of a sea-anemone, or medusa.

The essential structure of a *Hydra*, or Medusa, or of a Sea-anemone, as well as of each of the zooids of a very large group

of animals, Hydrozoa, etc., is that of a simple sac attached to some fixed object. The sac has one opening, or mouth, and this is fringed by tentacles. The sac, or cœlenteron is the nutritive cavity and food materials are taken into it by the tentacles, while indigestible débris is expelled *via* the same orifice.

11*d*. The Racemose–Hydra Type. In a vast number of kinds of animals, (very many of the Cœlenterata) the individual organism consists of a great number of segmental zooids, each of which has the essential structure indicated above.

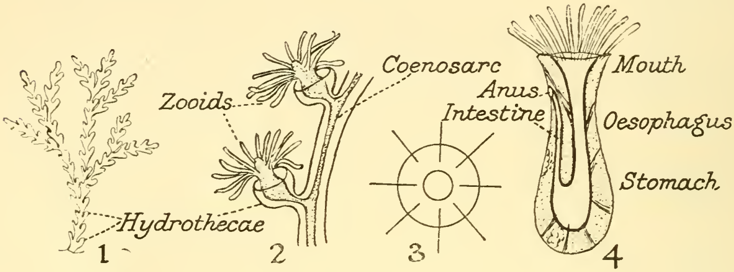


Fig. 6.

1, A Hydrozoon; 2, the same, only two Zooids being shown; 3, the radial symmetry of the Zooid, being the sac with its mouth-orifice and radial tentacles; 4, a Zooid belonging to the Polyzoa: here the symmetry is bilateral (there being mouth and anus) and radial (because of the tentacles). Racemose symmetry of the colony is shown in 1.

11*e*. The Polyzoan Type. This is represented in No. 4 of Fig. 6. The zooid in the Hydra type is essentially a sac built up of two main layers—the outer ectoderm, which is protective and aggressive (having stinging cells) and the inner endoderm which is nutritive in function. The symmetry of the zooid is radial. But in the animals called Polyzoa the middle layer of the body wall—the mesoderm—is much more highly differentiated than in the Hydra type, and the symmetry of the zooid is now bilateral, or right-left in respect of some of the organs.

11*f*. The Colonial Types. Changing our point of view, we now look upon many of the multicellular animals as being compounded of units, or segments, arranged in the racemose form indicated above, as well as in other forms. Thus the Hydrozoa, or Zoophytes are made up of zooids enclosed in little cups, or thecæ (No. 2 of Fig. 6) and these thecæ are arranged in branching forms, one of which is indicated in No. 1 of Fig. 6. Corals are examples of colonies of zooids of the Hydra type. Polyzoa are

animals which are colonies of zooids of the Polyzoan type. There are worm-colonies, ascidian colonies, etc. In all such cases the individual animal consists of the segmental zooids, which are often all nearly of the same structure, but often also the zooids are differentiated so that reproductive, nutritive, flotational, aggressive and other functions are specially performed by them. The zooids are always aggregated by some special substance, the horny material, or chitin, of the zoophytes, the massive, stony lime of the corals, etc. As a rule, also, the fleshy substances of all the zooids are joined by filaments, as shown in No. 2 of Fig. 6.

11*g*. THE ECHINODERM TYPE. This is best illustrated by the familiar starfish.

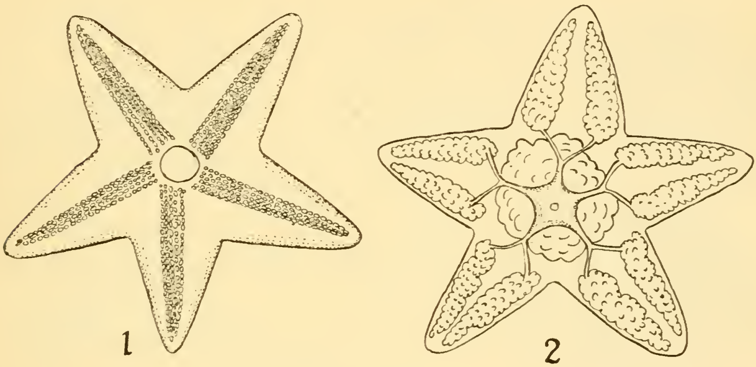


FIG. 7.

1, A Starfish seen from its lower side. The numerous small circles represent the locomotory organs, or "tube-feet"; 2, the same, seen from the upper side and dissected to show how the alimentary cavity extends radially into each of the arms. The other organs have also such a radial arrangement.

The sea starfishes, sea-urchins, sea-cucumbers, etc. (all the fossil species being included), form a homogeneous, well-defined animal type in which there is, in spite of apparent diversity of appearance, an essential similarity in structure. In all forms there is upper and lower, radial symmetry. The "arms" of the starfish, and the corresponding parts of the other forms, are segments each of which contains a similar, or nearly similar set of organs. Peculiar to the Echinoderms is the mode of locomotion by the suctorial "tube-feet."

11*h*. THE WORM TYPE. The earthworm, No. 2 of Fig. 9, illustrates the type. The term "Annelids," applied to many of

the most typical worms describes their outer form. The body is elongated, with typical triple-symmetry and it is often externally " ringed " because of its division into the metameric, fore-and-aft segments. The " worm "-group is far more heterogeneous than any of the others we consider here ; nevertheless, a large fraction of all the forms included in it have the essential structure displayed by the earth-worm.

11*i*. The Molluscan Type. A vast number of animal species belong to groups represented by the familiar forms, Bivalves (oyster, for example) Univalves (whelk, or periwinkle, or common snail, cuttlefish, etc. Examples are represented in the figure.

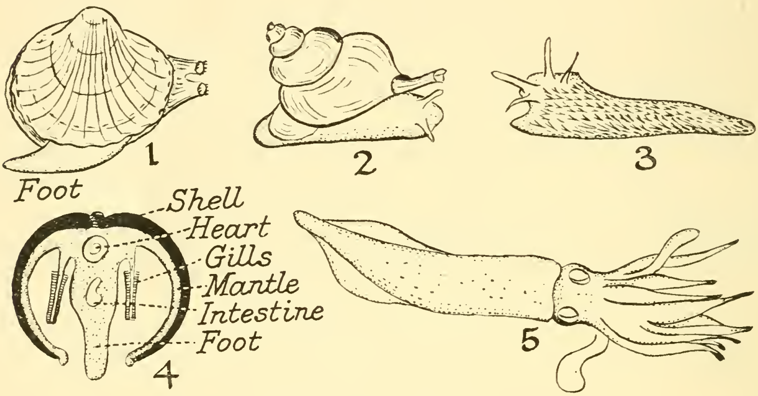


Fig. 8.

1, A Bivalve (or Lamellibranch), the Cockle ; 2, a Univalve (or Gasteropod) ; 3, another Univalve, a marine slug, or Nudibranch ; 4, transverse section through a Bivalve, such as the Cockle ; 5, a Squid (Cephalopod).

Here we have an animal type that is homogeneous in spite of much outer diversity of unessential nature. Typically, the mollusc is a soft-bodied animal partially enclosed in a shell of calcareous material. The symmetry is triple. Apparently very many molluscan bodies are unisegmental, but the actual, or concealed existence of the pluri-segmental body can be demonstrated. There is a strongly muscular part of the body (the " foot," for instance). The body is covered by a fleshy " mantle." The shell can be closed (in many groups) so as completely to enclose the body. The shell assumes most varied forms.

11*k*. The Arthropod Type. Arthropods include the Crus-

tacea, Insecta, Spiders, Mites, Myriapoda, etc. (taking account of the fossil forms). They are the most widely distributed of animals.

The Arthropod has a jointed body with jointed limbs, or appendages. The bodily joints divide the body into segments. The body is typically enclosed in a calcareous shell, or carapace. Exceptionally the limbs may be absent and there may be no hard carapace. Usually some, or (exceptionally) all of the segments coalesce. Typically each segment carries a pair of appendages

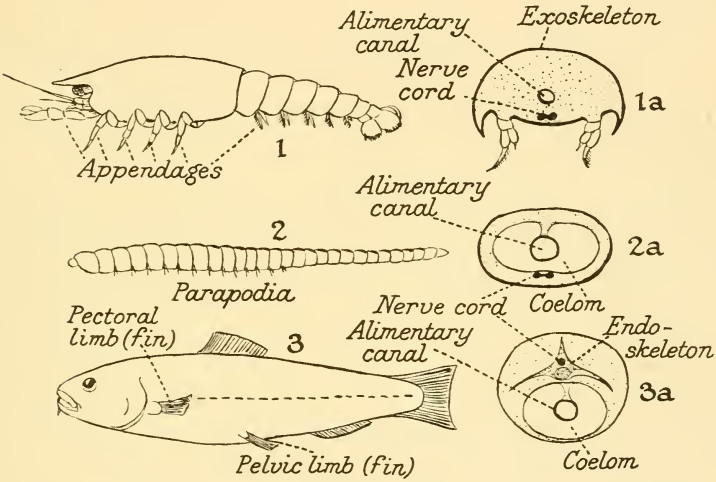


FIG. 9.

1, A crustacean; 1*a*, transverse section of the body of the same; 2, a worm; 2*a*, transverse section of the body of the same; 3, a vertebrate (fish); 3*a*, transverse section of the body of the same.

and the forms of the latter are usually modified for various purposes (walking, swimming, prehension, aggression, sensation, etc.). Symmetry is triple. In spite of the most extraordinary modifications the above essential structure is either obvious in the adult arthropod or can be seen in the embryogeny.

11*l*. THE CHORDATE TYPE. This includes the vertebrates, the tunicates and some other infrequently occurring forms. The symmetry is triple (with a curious radial arrangement in the Colonial Tunicates). The chordates are characterized by the presence of a notochord, which becomes the vertebral column. There is an internal limy endo-skeleton in most chordates in

contradistinction to the outer exo-skeleton of the arthropods. There are a number of " fore-and-aft " segments in the body of a vertebrate, even though the body may appear to be single and undivided. This fundamental segmentation is indicated (for instances) in the jointing of the vertebral column and in the repetitional arrangement of the nerves coming from the brain and spinal cord.

There are always four limbs :

Two pectoral and two pelvic fins in Fishes ;

Two fore-limbs and two hind-limbs in Amphibians and Reptiles ;

Two fore-limbs (wings) and two hind-limbs (legs) in Birds ;

Two fore-limbs and two hind-limbs in quadrupeds ;

Two arms and two legs in man and other Primates.

(But limbs may be quite absent in the adult stages (in some snakes, etc.).

There is a skull in most chordates and this is essentially a bony case enclosing the brain and partially enclosing the great head sense organs. There is a spinal canal in the vertebral column and this encloses the spinal cord. The whole central nervous system, brain and cord, is dorsal to the alimentary canal. (It is ventral to the latter in the worms and arthropods.) And so on.

In the above treatment of animal types we have, in the main, followed the lines of a rational classification of animals (see Section 94). But only slightly, since even a conspectus of the structural features of such a classification would be a lengthy matter. It would take account of extinct and degenerate species and larger groups ; it would weight all those structural characters that are indicative of phylogenetic relationships (Section 97) and it would tend to neglect such superficial (though perhaps very striking) structural features as indicate changed habits, some adaptations, degeneracy, parasitism, the assumption of colonial habits, etc. The basis of a rational classification is (so to speak) a " purged " morphology and we cannot (and need not) deal with it here. We are concerned with the existing appearances and activities of animals and, for the present, not at all with their genetic relations and evolution. Thus we look upon types of living things, categories into which we include the forms that are like each other (in general ways) in their modes of life, general bodily structures and physiologies.

Thus we may cut across the lines of a rational classification and consider such other life-types as the following:

11*m*. Colonial Types. (See Section 11*f*. "Colonies" of Hydrozoa or Polyzoa are, we have suggested, integrations of segmental parts. ("Integrations of the second order," Section 10*b*.) The "joints" of a worm, or lobster, for instance, are segments integrated into a body acting as a unity. So are the "arms" of a starfish. So also the zooids of an Antennularian, or of a Polyzoan are best regarded as segments with a very imperfect degree of integration (but in a Siphonophore the integration of the zooids is much more complete). Loosely, and from long usage, such Hydrozoan, Siphonophore, Polyzoan, etc., aggregates are called "Colonies."

Colonies of worms, of Salpidæ, etc., are rather different from the Cœlenterate and Polyzoan colonies. In the former the units that cohere, or associate, are already pluri-segmental animals. Here, then, in such latter colonies we have rather *communities* in which the integration is not merely the result of the combined behaviours of the units (as in a bee-hive) but there is actually structural adhesion of the units of a colony (as in the worm-groups, *Sabella*, or in a chain of Salpidæ). We might, perhaps, speak of such associations as "integrations of the third order": communities in which the nexus is structural rather than behaviouristic as in, say, the gregarious herd.

11*n*. Motile, Sedentary and Sessile Types. Motility of the animal is universally the case, *at some phase*, or throughout the individual life-history. The animal organism is, in general, able to move about and many species are characterized by very definite, seasoned migrations which they perform. Even if the adult animal is not motile its eggs or larvæ have powers of movement, or they are dispersed by being carried by water currents. This motility, or dispersal of the ova or larvæ ensures the distribution of the species over a wide region. There are sedentary animals (Mussels, Oysters, etc.) which throughout their adult lives do not move far from the places on the sea-bottom to which they are more or less rigidly adherent. There are truly sessile, "rooted" types, such as the Sponges, Zoophytes and Polyzoa which are attached permanently to the sea-bottom. Sedentary, semi-sedentary and sessile animals always have eggs and larvæ that are motile, or undergo dispersal. With the assumption of

the sedentary or sessile habit the structure becomes modified in so far as organs of locomotion are not at all, or are feebly developed.

110. Shelled Types. Many kinds of animals have bodies that are naked, in the sense that they are not covered with hair, scales, or other integumental, protective structures. Thus there are the naked Sea-anemones and Sponges, the Marine Nudibranch Molluscs, the Garden Slugs, etc. Many other forms are wholly or partially enclosed in a hard stony shell—the Oyster and other lamellibranch Molluscs, the common Barnacles, Whelks, etc., the Sea-urchins are examples. There are animals with bodies thickly covered with fur or feathers (as with most Mammals and Birds), or with scales (Fishes and Snakes) and so on. Such forms are intermediate, in a way, between the naked and shelled types. In general the shells, scales, fur, feathers, etc., are to be regarded as structures secreted by the skin, for protective purposes and they are permanent (as in the Molluscs) or may be cast off and renewed (as in the cases of the Crustaceans and many other animals).

11p. The Parasitic Types. Many groups of organisms have so evolved that they have lost the power (either wholly, or periodically, at some phase in their life-history) of independent life in open nature. They are resident as parasites, in or on the bodies of other animals. Examples of such groups are: many kinds of Bacteria and Moulds, Cestodes (or Tapeworms), Trematodes (Liver-flukes), Nematodes (Threadworms), etc. In these parasitic forms (and particularly those that have thoroughly evolved the parasitic habit) there are profound, and often bizarre, modifications of structure and habit. In all of them some notion of the free-living ancestral forms from which they have evolved can be made out from a study of the embryologies.

These types of animal bodies and structures are intended only to give some general idea of the forms of life in the most general sense. The study of phylogeny (or blood-relationships consequent upon the evolutionary process) demands a knowledge of rational classifications and the study of individual development means the investigation of embryonic structures. But for the study of organic functioning in general the investigation of structure (though it is always made) is not necessarily informative.

12. *ON THE ORGANS OF THE ANIMAL BODY*

The general motions of the animal body are the expressions of its behaviour. (This we consider more fully in a later Chapter.) These motions of the animal, as a whole, are made possible by the functioning of organs, which we regard, in the meantime, as quasi-independent mechanisms, integrated in various ways. Organs have morphological structure which it is convenient (from the point of vew of exposition) to study just as we have dealt with the animal structure as a whole. We consider, in a very summary way (1) the apparatus of movement; (2) organs of nutrition; (3) organs of respiration; (4) organs of circulation; (5) glandular organs; (6) organs of the nervous system and (7) sense-organs. But in a later Chapter we shall deal more fully with the nervous and sense-organs, and organs of reproduction form the subject of a separate Chapter.

12*a*. The Apparatus of Movement. This involves contractile tissues arranged, with skeletal parts, blood-vessels and nerves, as mechanisms appropriate for the particular motions in question.

In such a mechanism there is usually a part that moves ("moving bone" in Fig. 10, 1), and a part that is relatively fixed (the "fixed bone" in Fig. 10, 1). Flexor and extensor muscles, the contractile tissues, move the part in opposite directions. Blood-vessels carry food materials to the muscle and carry away waste products; these vessels also carry the oxygen necessary for the energy-transformations. Nerves transmit stimuli from the central nervous system to the muscles and blood-vessels. The skeletal parts to which the muscles are attached may be bones (in vertebrates), shells and carapaces, etc., in the invertebrates. Or there may be no skeletal parts (as in the "bells" of Medusæ, the iris of the eye, the walls of arteries, etc. The mechanisms vary in countless ways, but the parts are always such as we indicate here. The mechanisms are parts such as hands, limbs, claws, teeth and jaws, spines, etc.—that is organs for the purposes of locomotion, prehension, eating, aggression, etc.

Fig. 10, 2, shows the opening and closing mechanisms of a bivalve mollusc, that is, the ligament, or spring, that forces open the shell and the adductor muscle that closes the same. In 3 is shown the muscular and liquid (blood) pressure mechanisms that expand and retract the tentacles, proboscides, etc., of many

invertebrates ; the muscle pulls inward the tentacle in the same way as the finger of a glove can be turned " outside-in " ; blood injected into the cavity of the tentacle reverses this motion (4). Fig. 10, 5, represents a ciliary epithelium, where the separate " hairs," or cilia, " lash " and so move the part covered by the epithelium, and so on.

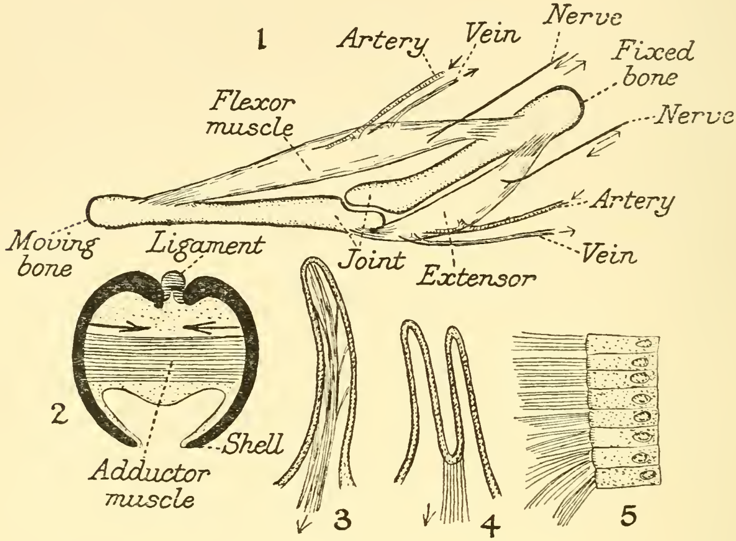


FIG. 10.

1, Diagram of part of the limb of a vertebrate ; 2, diagrammatic transverse section of a bivalve mollusc ; 3, a retractile tentacle fully expanded ; 4, the same partially retracted ; 5, a ciliary epithelium.

12*b*. ORGANS OF NUTRITION. The mechanisms just studied procure the food, which is then digested in alimentary cavities, intestines, stomachs, etc.

Food is taken into the alimentary cavity, which may be the simple cœlenteron of a Hydra (Fig. 5, 2), or the mouth, stomach and intestine of a vertebrate. Enzymes prepared by the glands digest the food. Blood-vessels circulating in the walls of the alimentary cavity absorb the digested food-materials. But there may be no alimentary cavity (as in a Tapeworm) and the animal then simply absorbs food materials through its integument. In such cases (which are usually those of parasites) the animal inhabits such media (intestine of some host-animal, etc.) where there are

present food substances that can be directly absorbed through the integument (being changed chemically in the processes of absorption).

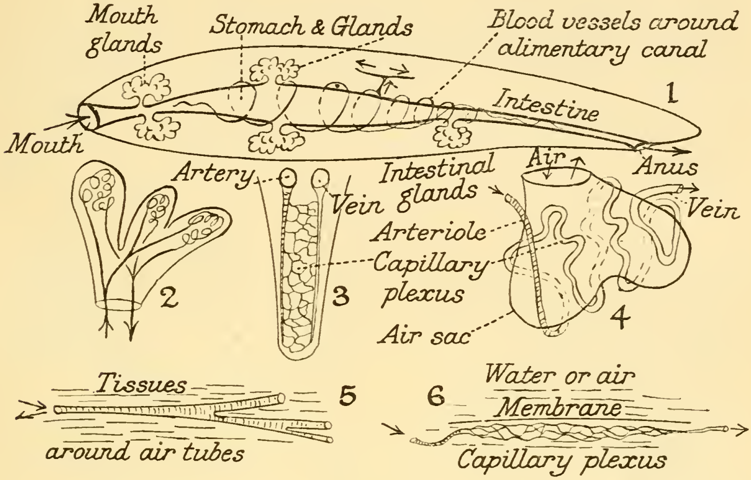


FIG. 11.

1, The alimentary canal, with its glands in a vertebrate; 2, a respiratory tentacle; 3, an element of the gill of a fish; 4, an air-sac in a mammalian lung; 5, a tracheal tube in an insect; 6, the essential respiratory mechanism.

12*c*. ORGANS OF RESPIRATION. In all cases there is a thin, semi-permeable, respiratory membrane. On one side of the membrane is the respiratory medium, air or water containing oxygen. On the other side is a plexus of blood-vessels. Oxygen is absorbed from the medium through the membrane and CO_2, etc., are extruded from the blood to the medium. This is the essential respiratory mechanism in lungs, gills, respiratory plumes, the tracheæ of insects, etc.

12*d*. ORGANS OF CIRCULATION. The fluid (blood) that carries nutritive materials to the organs of motion, etc., is conveyed by blood-vessels, arteries, capillaries, veins and channels of less definite formation. The fluid is propelled through the channels (blood-vascular system) by the pumping mechanism, or heart.

There are innumerable variants of such a mechanism: for instances, the heart may be double, triple or quadruple-

chambered. It may be associated with lungs, gills, ctenidia, etc., and so on, yet the system of a closed series of channels through which blood is propelled by a heart, is the essential structure.

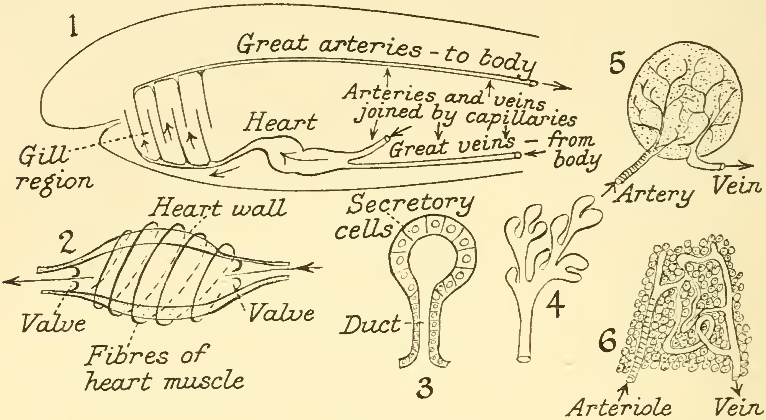


FIG. 12.

1, Diagram of the circulation in a fish; 2, diagram of the simple, one-chambered heart; 3, a simple gland; 4, a racemose gland; 5, a ductless gland; 6, blood capillaries ramifying through the cells of a gland.

12*e*. GLANDULAR ORGANS. Such are, for instances, salivary gastric, sweat glands, etc., kidneys, adrenal, thyroid, etc. glands. Whatever a gland may be, its essential structure is always this: there are secretory cells among, or outside, which blood-vessels ramify. Sometimes (and in general) the secretory cells enclose a cavity into which the secretion is poured (from the cells). Usually a duct carries away the secretion from the gland. The forms of the glands and ducts vary greatly. Sometimes there is no duct (thyroid) and then the secretion is carried in the blood that feeds the gland.

12*f*. ORGANS OF THE NERVOUS SYSTEM. In the cœlenterates the nervous system is a simple plexus, or network of nerves. This primitive nervous system also exists in the walls of the alimentary canal of the highest animals and it can effect complex reflex actions. Usually there is a central, ganglionic mass, or brain, or several such organs.

There are sense-organs and the essential element of such are the terminations of single nerve-fibres. From such a receptor a fibre passes into a nerve centre and another fibre passes out to

an effector organ. In the simple nerve-net, or diffuse nervous system, some of the elements of the latter are connected with receptors and others are connected with muscles, or other effector organs. In the higher animals there is a centralized nervous system, or systems, and these central parts are the ganglia. Nerves leading into the ganglia are afferent nerves and those leading out are efferent nerves. The brain of the vertebrates is an aggregate of ganglia. The cerebral ganglia of the invertebrates corresponds

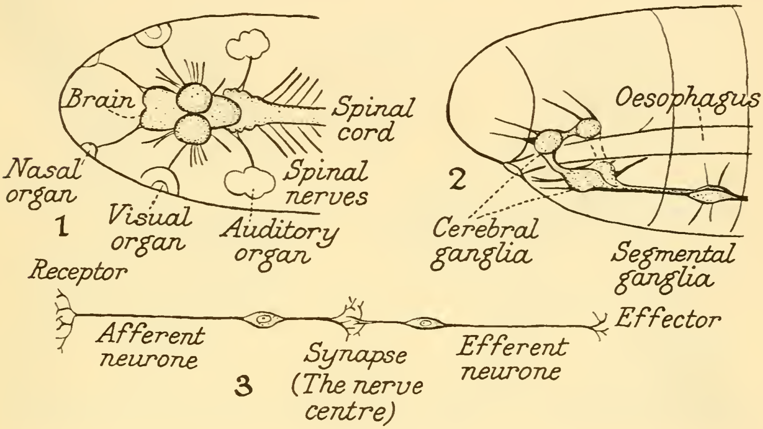


FIG. 13.

1, Diagram of the central nervous system of a vertebrate; 2, diagram of the central nervous system of a worm; 3, an element of the nervous system of a vertebrate.

with the vertebrate brain. The element of the whole nervous system of either the vertebrate brain or the invertebrate nerve-centre consists of at least two neurones (see Section 13 and No. 3 of Fig. 13).

12g. THE SENSE-ORGANS. Whatever it may be, a sense-organ consists of one or more receptors. A simple receptor is the branched, or otherwise modified termination of a nerve-fibre and these terminations are situated in the skin, or in some other bodily part where physical stimuli impinge upon them. As a rule the nerve-terminations are provided with accessory parts: thus the visual receptors are the nerve-terminations in the retina of the eye, but the eyeball, the lens, the iris, etc., are the accessory parts which modify and direct the stimuli impinging on the nerve-terminations.

13. *ON ORGANIC TISSUES*

Whatever they are, the bodily organs are aggregates of tissues. An organ is a definite tectonic arrangement of many kinds of tissues. Thus the eye of a vertebrate is built up of skeletal tissue (the sclerotic), nervous tissue (the retina), vascular tissue (the blood-vessels), etc. Tissues are aggregates of differentiated cells.

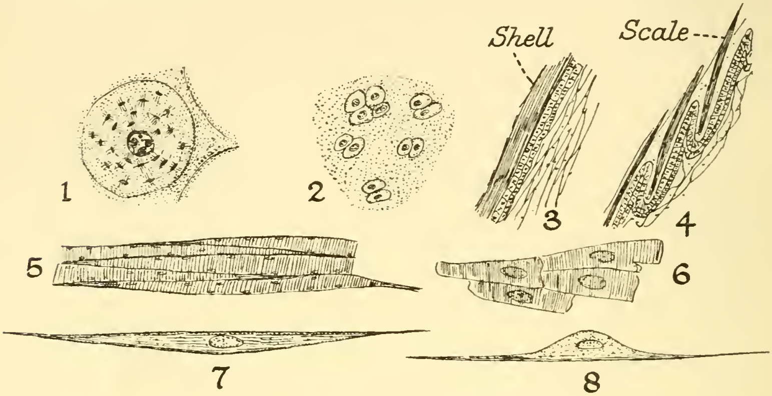


FIG. 14.

1, Bone tissue ; 2, cartilage ; 3, the shell, or carapace of an invertebrate ; 4, the skin of a fish, showing the scales ; 5, striated muscle-fibres ; 6, muscle-fibres from the heart of a vertebrate ; 7, an involuntary (unstriated) muscle-fibre ; 8, a muscle-fibre from a Trematode.

Skeletal Tissues. It is customary to speak of the " Living " cells (such as bone-corpuscles) that secrete the matrices and the non-living substance of the latter. This distinction is not always clear, for it may not be possible to decide in what way a thick cell-wall differs from an inter-cellular matrix, and it may not be possible to decide whether or not a cell-wall is any less alive than other parts of the cytoplasm. Cartilage has cells imbedded in it. Bone is a matrix containing cells and cell-filaments. In all cases a skeletal tissue, bone, cartilage, shell, etc., has a framework of cells that secrete the substance of the matrix.

Muscular tissue. A muscle is an organ which has in it muscle-cells, nerves, blood-vessels, lymph vessels and connective tissue. The characteristic and most prevalent tissue consists of arranged muscle-cells. In the muscle these cells are compacted together by their own external membranes and by interstitial connective tissue. It is, of course, the co-ordinated contractions of all, or

many, of the cells in a muscle that initiate the tension of the latter (see Nos. 5–8, Fig. 14).

Nervous tissue. Everywhere in ganglionic centres and nerves the elements are nerve-cells (see Section 41). Nerve-cells, or neurones, in various modifications, constitute the central and peripheral parts. Everywhere nerve fibres and nerve-cells are bound together by connective tissue (see No. 3, Fig. 13).

Glandular and metabolic tissue. The units are cells of various forms (see Nos. 3–6, Fig. 12).

Vascular tissue. Such is that making up the tubes which carry blood, lymph, etc. Arteries, veins and capillaries are really

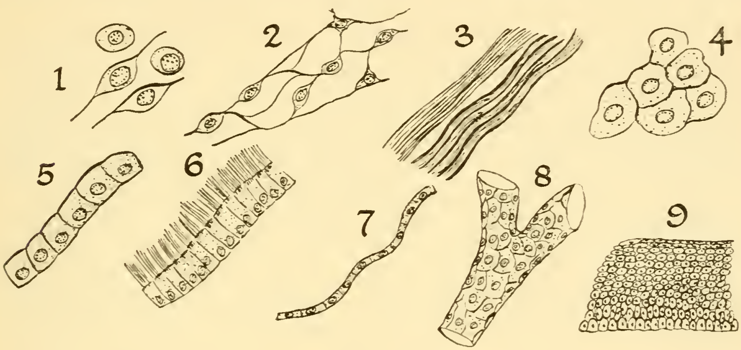


FIG. 15.

1, Connective tissue corpuscles; 2, areolar connective tissue; 3, fibrous connective tissue; 4, a squamous epithelium; 5, a cubical-celled epithelium; 6, a ciliated epithelium; 7, a "pavement" epithelium; 8, squamous epithelial cells forming the wall of a blood capillary vessel; 9, an epidermis.

organs. Thus an artery has a complex wall in which are both muscles and nerves. But it is convenient to think about connective tissue as being modified to form the small veins and capillaries as well as the obscure channels through which blood and other circulating fluids pass in the lower animals and, in a sense, there is a tubular or vascular kind of connective tissue. (No. 8 of Fig. 15.)

Epithelial tissue. This consists of layers of cells that form sheets. These epithelia, or sheets, line internal cavities, the body cavity, the mouth, the bladder, heart, arteries and veins, etc. The epithelia may be glandular (Fig. 15).

Epidermal tissue (No. 9 of Fig. 15). The external layers of integument comprise this.

Connective tissue (Fig. 15). This consists of the ubiquitous

tissue that binds together other tissues and organs, that acts as a packing between organs and parts of such, that suspends organs in the body cavity ; that joins muscles to their bones, etc.

14. *ON ANIMAL STRUCTURE IN GENERAL*

There are animal forms, each form being typical of a category (see Section 77). Such forms are indefinitely numerous. So also there is an indefinitely great number of patterns of animal behaviour.

But if we regard the structure of the body of an animal as that of a system of parts, or a physico-chemical mechanism that subserves the activities of behaviour, we find that :

> *The number of essential structural patterns is very much less than the number of animal forms.*

Thus the alimentary system (mouth and teeth, salivary glands, œsophagus, stomach and gastric glands, intestine and intestinal glands, liver, spleen, pancreas, etc.) is very much the same, and does very much the same things in all vertebrate animals.

[The analogy is with the multitude of makes of automobiles that one sees on the roads. These differ in size, accommodation, general elegance, finish, etc. But as mechanisms their essential structures are far fewer than the number of " different " makes of cars].

In the animal body there are organs—brain and nervous system, muscular organs, glandular organs, etc. But the number of essentially different organs (different in the way that the fish-gill, as a respiratory organ, differs from the mammalian lung) is relatively small.

Smaller still is the number of different kinds of tissues and tissue-cells. In the last resort the characteristic activity of an organ is the activities of its characteristic tissue-cells.

14*a*. Structure in Relation to Functioning. There is not a close one-to-one correspondence between the structure of an organ and the things that that organ does. Thus the result of activity of a respiratory organ is the oxygenation of the blood, but the fish-gill does that as adequately (from the point of view of the fish) as do the lungs of a mammal. That is, mechanisms that are *externally or superficially* different in structure may do the same things, in the functional sense.

In this case (the fish-gill and mammalian lung) the essential mechanism is a red-blood-corpuscle, containing hæmoglobin, that absorbs oxygen. In the fish-gill there is oxygen in the water that bathes the membranes behind which is the fish blood-stream. In the mammalian lung there is oxygen in the cavity that is lined by a membrane, behind which is the mammal's blood-stream.

14*b*. Unessential Structure. Details of animal structure may be quite unessential to the bodily behaviour or to organic functioning. Such details are, in a way, superfluous, or excess, structural details. For example, the Herring and Pilchard have the same general habits and methods of nutrition and they have analogous migrations and nearly similar modes of reproduction. Yet the Pilchard has large and relatively thick scales while the Herring has much smaller ones. Such a difference in structure has no counterpart in functioning that we know, yet it is constant and it is perfectly diagnostic of the specific, morphological differences in the two species of fish.

14*c*. Chemical and Morphological Structure. Only in the most general way does chemical composition determine morphological structure. In the large vertebrates (whales, the extinct Dinosaurs, etc.) a very strong internal skeleton is necessary to support the weight of flesh. Such a skeleton must involve some such substance as lime, silica or perhaps ferrous hydroxides or carbonates. Lime, of course, is actually used.

But vast numbers of zoophytes have chitinous exoskeletons and the chemistry of the soft parts of their bodies is the same in all species, so far as we know. Yet the morphological differences in these groups are very great.

It is easy to see that there need not be an invariable relation between chemical composition and animal morphological characters. By analogy we may make this clear (for the chemistry of the animal body is inconclusive in regard to the problem). Very many patterns may be stamped out on the same coin blanks and it is the construction of the dies, not the nature of the metallic discs, that determines the patterns.

Yet, on similar analogies, there may be a necessary relation between structure and material: it would not, obviously, be possible to construct such a fabric as the Eiffel Tower from bricks and mortar.

14*d*. Excess-Values in Animal Structure. Regarded as mechanisms, animal structures need not exceed a certain degree of complexity. But in colours, patterns or pigment, forms and sculpturings on shells, frustules and other external hard parts, feathering, plumes and crests, fantastic bodily forms, etc., we seem to see what we, as artisans, should call " ornament " and over-elaboration : structural detail that is, so far as we can find by experiment and observation, unnecessary for the effect that the bodily part or organ may produce in order that the general behaviour of the animal may be subserved. This is " excess-value."

15. *ON ANIMAL STRUCTURE AND ITS SIGNIFICANCE IN GENERAL BIOLOGY*

15*a*. Structural Mechanisms. We may here regard a mechanism as a system of parts that are placed in relation to each other in a definite way. When these parts are actuated a certain definite effect follows and the nature of this effect depends on the ways that the parts of the machine are placed in relation to each other.

Thus the human arm is such a system of parts. Shoulder-blade and humerus are so articulated that the latter moves in a ball and socket joint. The forearm bone (the ulna) is so articulated with the humerus that a hinge joint is formed : thus the natures of the movements of humerus and forearm that are possible are determined by the natures of these articulations. Muscles are attached between the various bones in such ways that their tensions apply forces to those bones. Finally, the muscles are energized. Essentially we have systems of levers, in the mechanical sense.

All the grosser mechanisms of the animal body can be described in analogous ways.

In the earlier conceptions of the animal body as a machine it was such mechanical (in the classic sense) conceptions that were made. But later speculations extended the notion of parts of a mechanism to physical systems containing tubes of varying calibre through which liquids flowed ; filters with pores of varying size ; liquids, quasi-liquids and gases (the " spirits ") that were expanded or contracted when the temperature varied and so on.

Thus, what we call, in ordinary language, *physical* structure

became part of the notion of the animal mechanism in addition to structure in the old-fashioned, mechanical sense.

Chemical structure. Later still chemical ideas were made. The muscles, nerves, bones, glands, circulating fluids, etc., had definite chemical structure. When the parts of the mechanism (now a physical-chemical one) were actuated the effects that followed depended on the chemical structure as well as on the ways in which the *visible* parts of the machine were placed in relation to each other. Perhaps the idea of a machine as stated above may hold valid with regard to chemical systems: the properties of the latter depend on the ways in which the atoms of chemical compounds are placed in relation to each other.

Microscopical structure. Study of gross structure did not carry the early physiologists very far: Thus Galenic physiology supposed that blood passed through pores in the septum between the right and left ventricles of the heart, although these pores could not be seen: they were parts of an assumed invisible structure. Later, of course, study of morphological structure, assisted by the microscope, showed that the pores did not exist but that blood passed from right to left sides of the heart by means of previously invisible vessels—the capillaries.

So in the early part of the nineteenth century much was expected to be learned as to organic functioning by the study of microscopic structure.

Ultra-microscopic structure. Even now much of our notions of functioning is based on structure that is ultra-microscopic but still assumed to exist. Thus there are viruses that are supposed to be structural entities but which are beyond the range of the microscope. So are the genes of the mendelians (see Section 81*d*). Like the Galenic ventricular pores, these are assumed in explanations.

Chemical structure is, of course, ultra-microscopic. Such constitutional formulæ as are quoted in Section 8 can hardly be regarded as other than convenient symbols that are most useful in explaining (or rather, describing) chemical reactions. Enzymes are only quasi-chemical entities and even a symbolism, such as that used to describe proteins, cannot be framed to describe their structure (if they have definite chemical individuality in the sense that the proteins have such).

Cellular structure and functioning. And in the last resort the

analysis of the functioning of an organ reduces to the processes that take place in the bodies and nuclei of the characteristic cells. We shall see, of course, that individual cell activities in an organ are integrated and that even the activities of organs and organ-systems are integrated. Nevertheless the activities of a muscle reduce to the activities that proceed in the individual muscle-fibres, or cells, and the secretion of saliva by the sub-maxillary gland reduces to activities that are, in the main, those that occur in the cells that form the gland acini.

15*b*. Structure and Phylogeny. The matter of the preceding sections deals only with the main kinds of animal structure, apart from any hypotheses of the ways in which those types of structure have evolved. Also it suggests what are the animal bodily parts that we shall regard as functioning in the following sections.

But much interest in animal morphology centres round classifications. The ways in which systematists arrange animals into species, genera, families, classes and phyla depend upon structure. Phylogenies show in what ways all the races, species, genera, etc., are related and how one race, species, etc., has evolved from some other one: They are "family trees." Structure, whether studied in the embryos and adult forms of recent animals, or in the fossils of extinct ones, appears to be the only way in which it may be possible to trace out evolutionary histories.

CHAPTER III

ORGANIC FUNCTIONING

By the term *Behaviour* is meant all the ordinary activities, and chiefly motions, of the living animal considered as a unitary thing. Thus its locomotions, actions of aggression and defence, the pursuit and capture of its prey, the seeking of shelter, making nests, the construction of artifacts, its play and courtship, etc., are examples of behaviour.

The limbs, wings, fins and other bodily appendages, the jaws, teeth, claws, spines, etc., are the *agents of behaviour.* These agents are actuated by systems of muscles, which are attached in various ways to bones and other relatively rigid parts, on the one hand, and to the movable instruments of behaviour (as the human hands and fingers) on the other. The muscles can be thrown into states of tension so that forces are applied to the instruments of behaviour. Such forces are initiated and regulated by the central and peripheral nervous systems, by the organs of sense and by the experience of the animal (see further in Section 39).

The instruments of behaviour are mechanisms of skeleton, muscle and nerve : These we may call *action-systems* and their forms depend on the general structural plans of the animals considered.

The action-systems are *energized* by the organs of alimentation, respiration and circulation—that is, by all the mechanisms that digest and assimilate food materials—thus obtaining substances that have energy ; by the oxygen taken into the body and by the heart and blood-vessels that distribute these materials throughout the body. Further *metabolic organs* preserve a general balance in the chemical constitution of the body.

Thus we may speak of the *energizing system*, and *the metabolic system* of bodily organs. The general activities of these parts may be called *organic functioning* : this is, of course, subservient to behaviour.

The *accessory activities of reproduction* are individual ones: thus courtship, copulatory actions, spawning, parturition and the nutrition and care for the progeny are to be regarded as individual behaviour. But the *essential acts of reproduction*—that is, the divisions and maturations of the germ-cells, etc., are racial activities and will be discussed specially (see Sections 65, 66).

So also the processes of sensation, of central nervous activities, of cerebral co-ordination, of ancestral and individual experience and of memory must be discussed specially (Chapter IV).

In the study of organic functioning, as it is taken up in this chapter, we deal largely with energy-transformations. Therefore a preamble on energy in general is necessary and to this we proceed immediately.

I. A PREAMBLE ON ENERGY

16. *ENERGY IN GENERAL*

There is a necessary condition that any physical change whatever may occur: this is the existence of available energy in the system of things in which the change occurs.

Thus available energy is, in the ordinary sense, the cause of physical changes, and when we measure the quantity of it that is contained in a system of things we also measure the quantity of physical causality exhibited by the system.

Energy (still in the available mode) is recognized by us in these states of things:

(*i*) *In the familiar world.* In the rotation of the earth, the gravitational attraction on earthly things exercised by the sun and moon, and in the heat of the sun—these conditions give us the tides, ocean currents, winds, running water, glaciers and icebergs; in the gravitation of things to the earth itself.

In atmospheric electricity and terrestrial magnetism;

In the internal heat of the earth that comes from its original condition and from the radioactivity of its materials;

In the chemical substances of the earth's crust and waters and atmosphere; coal, oil and all the materials that can interact with each other; and so on.

(*ii*) *In the outer universe.* In the radiant energy of the stars, appearing to us as light and heat ;

In cosmic radiations traversing space in all directions ;

In universal gravitation.

17. *ON MATERIAL THINGS AND ENERGIES*

The universe is constituted by material things and energies (this statement is of the nature of a first approximation). Whatever they may be, material things are constituted by about ninety-five different kinds of chemical atoms.

Whatever kinds they may be, the chemical atoms are constituted by protons and electrons.

Electrons are indivisible, excessively minute charges of electricity, negative in their sign. Protons are corpuscles constituted in some unknown way and exhibiting a positive sign. In some way protons become aggregated to form the nuclei of atoms and round the atomic nucleus there is an " atmosphere " of " satellite " electrons. The latter are distributed in " orbits," but close to the nucleus an electron fills the whole orbit. At a great distance from the nucleus the satellite electrons behave as particles which are regarded as revolving round the nucleus in orbits. They may also behave as *waves.* There can only be a limited number of such orbits and an electron can change its orbit. But it disappears from one orbit and simultaneously appears in another rather than " jumps " from one orbit to another.

Different kinds of atoms are characterized by having different numbers of protons in their nuclei and different numbers of satellite electrons.

Protons and electrons are electricity and electricity implies energy. Therefore the physical substance of the universe is energy.

18. *ON RADIATION*

Radiation is energy that is not inherent in, or immediately associated with material bodies. Familiar examples are :

The heat felt when one stands near a fire ;

The light coming from the sun ;

Wireless signals.

18*a*. FIELDS OF FORCE. There is said to be magnetism in

a magnetized steel bar, but in the neighbourhood of such a magnet a compass needle is deflected ; this neighbourhood is the seat of a field of magnetic force ;

Round a wireless station receiving sets are affected and respond ; in this neighbourhood there is an electro-magnetic field of force ;

Round the earth there is a gravitational field (but this is not of the same nature as magnetic or electro-magnetic fields. In the neighbourhood of massive bodies other things that have mass move in certain ways.

Let the circle E in the following diagram represent an electrically charged body :

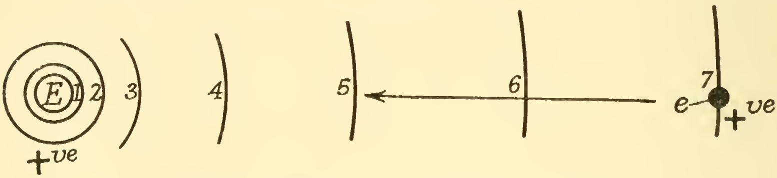


Fig. 16.—Diagram of a Field of Force.

The electric charge is not only *on* the body, but it also exists *all* round it to an indefinitely great distance. The concentric circles 1–7, represent imaginary boundaries in this field of electrostatic force. At 7 there is a body, E, carrying a small test charge : if we move *e* from, say, 7 to 5 work is done upon it. The quantity of this work measures the intensity of the charge on E, as it is experienced at *e*. The intensity of the field decreases as we pass outwards from E, for the charge is always being distributed over an increasingly great region.

It " takes time " to build up such a field of force. If E were to be suddenly discharged the field would " collapse " sooner at, say, 5 than it does at 7. Therefore *a field of force has extension both in space and time.*

18*b*. Oscillators. In many systems the intensity of the included energy regularly decreases and increases, or undergoes regularly repeated transformations. Thus a " Hertzian oscillator " is two spheres near each other and charged with electricity up to sparking-point (the field round them is no longer electrostatic). Consider the events :

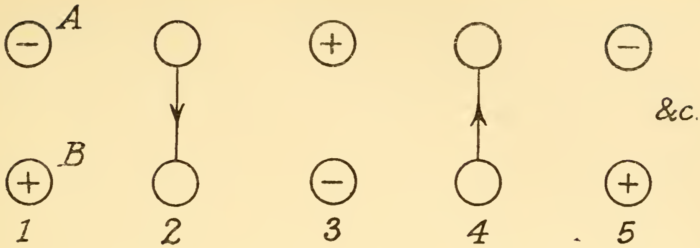


FIG. 17.—DIAGRAM OF A HERTZIAN OSCILLATOR.

When the charges become too great they "spark across" (2), and then the inertia of the current causes the polarity to be reversed (3), again the charge sparks (4), and again the polarity becomes reversed (5). These alternations may occur at the rate of several millions of times per second. Every time they occur the electro-magnetic field round the oscillator changes and it changes sooner after an oscillation between A and B at some place near the latter than at some place far away. A change occurring at A and B would be followed a second later by a change in the electro-magnetic field 300,000 kilometres distant, at a place 600,000 kilometres away two seconds later and so on.

Cycles of changes at the centre of the field affect *all* the field, but these cycles in the field are perceived later in time than they occur at the centre. Everywhere in the field the cycle of changes is similar in form to the cycle at the centre, but the amplitude of the cyclic change falls off as we pass out from the centre. If we plot graphically the regular increase and decrease of energy at some place in the field it is represented by a "wave," as shown in Fig 18 on page 60, and we say, for convenience, that pulses of energy occur in the field.

18*c*. RADIANT ENERGY. Such pulses of energy appear *to be emitted* from a source. If we represent them graphically (as in the above diagram) a train of waves, each with a certain "wave-length" appears to radiate out from the oscillating system. Thus waves of light are said to be emitted by a luminous substance; electro-magnetic waves from an oscillating thermionic valve and so on. The lengths of the waves vary (10^{-8} cm. from an X-ray tube and 1,554 metres from the wireless station called 5 XX). The frequencies of occurrence per second of these waves is very variable, but the velocity with which they appear to be emitted

is always the same. They are imagined as being analogous to the visible waves in water and they are sometimes said to be "transmitted" by the ether of space. All this is a convenient way of speaking about radiation, but it is only a convenient fiction.

Most physical systems have fields of force round about them and extending to an indefinite distance. This just means that such physical things are wherever they can be detected because

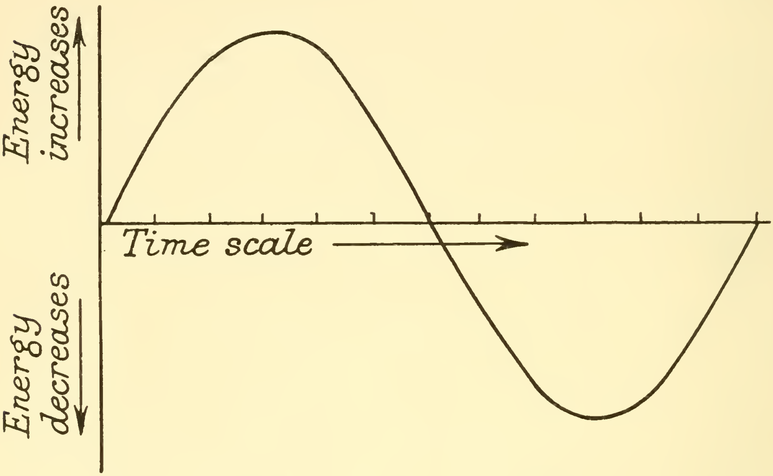


FIG. 18.—DIAGRAM SHOWING VARIATIONS IN THE INTENSITY AT A POINT IN A FIELD OF FORCE.

we do not now postulate an ether of space in which radiant energy is propagated. When the physical thing oscillates the field of force surrounding it also oscillates.

19. *ON THE MODES OF ENERGY*

It will be convenient, for the purpose of exposition, to regard energy as existent in three "modes":

19*a*. AS BOUND ENERGY. This is the energy of protons and electrons that are so assembled as to form the atoms of permanent matter. In our present experience it is impossible, by any means, to cause these atoms to break up, or disintegrate, so that the energy that holds the protons and electrons together may become free. (It *is* possible to break up a nitrogen atom, say, by

bombardment, but we neglect this, so far, very exceptional result.)

19*b*. As Free, or Available Energy. This is energy in such a mode that it may become the reason, or cause, or condition of the occurrence of physical changes, we know it as—

The energy of massive material bodies such as winds, running water ; heavy bodies that are actually falling to earth, or gravitating ; material things in motion such as the flywheel of an engine, a locomotive or a motor-car ; the actual movements of uncoiling of a spring ;

the energy of the molecules of material bodies that are moving so rapidly as to be hot ;

the pressure of the molecules of a gas that is confined, such as steam in a boiler ;

the mechanical pressure of radiation, such as light ; gravitational energy such as that of a mass of water contained in an elevated tank, or the energy of the weights of a clock ;

the chemical energy of many substances such as coal, oil, oxygen, etc. When such substances react chemically energy in the form of heat, electricity, etc., becomes manifest ;

the energy of a magnetic body ; electric energy ;

radiant energy such as light, heat, electromagnetism, X-rays, etc. ; the energy of radio-active substances.

All such energies are free to become transformed and, in so doing, they set up physical changes.

19*c*. Unavailable, or Dissipated Energy. This is energy which, from the present, human point of view, cannot be made to transform so as to set up what we call here physical changes. It is—for instances :

the energy of motion of the earth and moon in their revolutions and rotations (but see Sections 5, 19*d*) ;

the energy of low-temperature heat such as that of the ocean ;

much cosmic radiation (see Section 89).

19*d*. Relativity of the Modes of Energy. Further consideration will show that the modes of energy are, to some extent, relative to human power of control. Before 1900 there was no available energy in uranium (or man did not know that there was available energy in this material—and this statement means the same thing as the previous one). At present there is no available energy in lead, but this statement may not be true at

some time in the future—when it *may* be possible to accelerate the radio-active disintegrations of bound atoms.

At present man cannot make use of the energy of motion of the molecules of sea water at its natural temperature. But it is conceivable that some marine bacteria can do so.

20. *ON THE FORMS OF ENERGY WHICH IS AVAILABLE*

Energy which is available—that is, which can set up physical changes—exists in many forms: Thus we know—

The energy of motion, or of state, of material bodies, as, for examples, the mechanical energy of moving bodies or machines such as heat engines; the mechanical energy of winds and rivers; the mechanical energy of a raised weight, or a coiled spring, etc.;

the energy of heat;

chemical energy, such as that manifested in combustions and explosions, etc.;

electric energy; magnetism;

radiation.

20*a*. Energy-transformations. Whenever any physical change, event, artificial phenomenon, or natural occurrence takes place the available energy of the system which we observe undergoes transformation. Examples are:

(*i*) Coal is burned in the furnace of a steam-engine (chemical energy transforms into heat);

(*ii*) heat (via the generated steam) actuates the engine (the energy of the microscopic molecules of steam transforms into the energy of the macroscopic material bodies (cranks, wheels, etc.) of the engine;

(*iii*) the engine rotates a dynamo and the rotation of the parts of the latter establishes magnetic fields; conductors move in these fields and electric currents are set up in them (mechanical, transforms into magnetic and electric energies);

(*iv*) the dynamo sends currents through the motors of a tramcar (electric, transforms into mechanical energy);

(*v*) the current passes through a glow lamp (electric, transforms into radiant (light) energy;

(*vi*) the current charges an accumulator (electric, transforms into chemical energy).

Solar radiation transforms into the chemical energy of the cellulose of green plants;

And so on, almost *ad infinitum*. The events that we call physical changes *are* energy-transformations.

20*b*. Transformers. In all such cases there is some system of things by reason of which the energy-transformation occurs. Such systems are :

Heat engines ; dynamos ; glow lamps ; accumulators ; electric motors ; the living cells of green plants, etc.

21. *ON THE PHASES OF ENERGY IN THE AVAILABLE FORMS*

Available energy may be *kinetic or potential.*

Kinetic Energy is that of the motion of physical things that have *mass*. Thus :

The energies of the moving parts of steam-engines, electric motors, vehicles, projectiles, etc. ;

the energy of the molecules of bodies that are hot—it is because of this kinetic molecular motion that we recognize heat ;

the energy of radiation : The " waves " of light, etc.—that is, the periodic changes in the intensity of an electro-magnetic field, have mass ; light can cause very small particles to move (this is " radiation pressure ").

21*a*. Potential Energy is energy that exists and is available but which is not manifest until it is *released*. Thus : the gravitational energy of a heavy body which is at rest but which is free to fall when released (the weights of a clock which is at rest) ; the energy of stress of a coiled spring (that, for instance of a clock or watch at rest) ;

chemical energy : which is that of the positions and linkages of atoms or molecules in relation to each other—thus the atoms of carbon and hydrogen in coal gas, and those of oxygen in the atmosphere are so arranged that they are free to react with other so that CO_2 and OH_2 are formed. In this reaction the potential energy of the reactants (the hydrocarbon and oxygen) becomes the kinetic energy of the resultants (CO_2 and OH_2). Motions of translation and oscillation are exhibited by these energized molecules and oscillatory motions of their electrons also occur. This kinetic energy we recognize as heat and light.

21*b*. Releasing Transformations. Generally potential energy passes into some other form, or into kinetic energy after a releasing transformation occurs. Thus :

the movement of a trigger mechanism fires a gun ; an initial swing of the pendulum of a clock at rest initiates the fall of the weights and the actuation of the mechanism ; a small spark ignites the explosive mixture in the cylinder of a gas engine ; a nervous impulse causes substances in the muscles of a man to disintegrate, so that the fibres contract ; and so on.

The quantity of energy involved in a releasing transformation is always small relatively to that involved in the main transformation. Also there is no proportionality between the two transformations.

22. *ON THE LAWS OF ENERGETICS*

22a. The Law of Physical Becoming. By " physical becoming " is meant the occurrences of energy-transformation which are manifest to us as physical changes, or " phenomena " (in the ordinary sense of the word). Such transformations have sequence and direction such that in their occurrences the function called *entropy* increases in value (see Section 22*e*). Such events differ from those that must characterize a physically " dead " universe (see Section 2*e*) in a way that is analogous to that in which vector quantities differ from scalar quantities.

In order that physical becoming may exist, available energy must be present in the system of things considered. Or, putting the matter in ways that mean the same thing, there must be differences of energy-intensity or potential ; or there must be " organization " of energies (see further in Section 4).

22b. The Law of Conservation. In the classical physics (of half a century ago) matter was said to be conserved—that is, did not ever originate and was incapable of being annihilated. But since the discovery of radio-active disintegration of some chemical atoms the precision of this " Law " has disappeared, for in such processes matter clearly disappears.

Mass, that is the " property " of inertia of crude matter, or of electro-magnetic entities, was said to be conserved, but quantity of mass is now known to be relative to the velocity of motion of an entity known to have mass.

However, since in radio-active transformations lost matter is quantitatively replaced by energy ; and since change of mass that is relative to something else can be explained away by mathe-

matical artifices; it is obvious that the law of conservation is not necessarily invalidated.

In the familiar sense available energy is the capacity for setting up physical change—"for doing work." But it is familiar experience that energy in this sense can "be expended." Therefore it would appear that it is not conserved. But available energy that disappears can always be accounted for: kinetic energy may appear to be lost, but it may only pass into the potential phase. Further, energy that is "expended" becomes "unavailable" (see Section 22*f*) and can still be traced. Therefore, again, the law of conservation is preserved.

Clearly the "law" of conservation is of the nature of a stipulation made by scientific method. No scientific result can possibly invalidate it, since it is a necessary element of scientific method itself. Thus dreams, hallucinations, phantasms, and perhaps "spooks" are "real while they last." But they cannot be "reduced to order"; they are a nuisance to physical science and they are dismissed from the domain of physical research—*because they are not conserved.*

All the same the invalidity, in the most precise sense, of the law of conservation does not apply to experimental biology—*in its present phase.* Presently we shall see that, so far as we can investigate the processes of organic functioning, using (as we still must use) the instruments of nineteenth-century physics, the classical laws hold good. Yet again, will that always be the limitation of biology?

22*c*. THE ENTROPY-LAW. This is the fundamental generalization of science—it is notable that the physical-mathematical revolution of the last twenty years has not shaken it in the least. The law of conservation we may regard as a logical category (just yet, at all events, for innate "laws" of thought are, no doubt, evolving just as bodily structure evolves). But the entropy-law appears to crystallize our knowledge that comes from sensory data.

It is so very general that we can approach it from various ways.

22*d*. IN ALL ENERGY-TRANSFORMATIONS AVAILABLE ENERGY DISAPPEARS. Some energy-transformations are (in the experimental sense) truly quantitative ones—that is, the energy of the system, before the transformation occurred, is precisely measurable and is the same as the energy (also precisely measurable) after the transformation occurred.

(*a*) Thus a falling weight is made to rotate paddle-wheels in a calorimeter (see Section 38). In falling the potential energy of the weight transforms into the kinetic energy of the rotating paddle-wheel and this latter energy transforms, by friction, into heat so that the water of the calorimeter rises in temperature. We cannot trace any other change than this and we say that *all* the available energy of the falling weight transforms into heat energy. This is the first law of thermo-dynamics, *or* the law of conservation. When a weight of 1 kilogram falls freely through a distance of 424 metres its loss of potential energy is equivalent to the quantity of energy that is necessary in order that the temperature of 1 kilogram of water may be raised by 1° C. But suppose that in falling some of the potential energy of the weight transforms into some other energy-form unrecognized by us but which may be detected in the future: in that case we should simply alter the measure of equivalence and the law of conservation will still hold good.

(*b*) In analogous ways other quantities of energy—chemical, electrical, etc., can be made to transform wholly into heat. If M units of mechanical energy, C units of chemical energy, E units of electric energy all transform wholly into Q units of heat energy then M, C, and E are equivalent.

(*c*) But suppose that M units of mechanical energy are made to transform as completely as possible into electric energy: then we shall not observe the above equivalence, that is, we shall not observe E units of electricity come out of the transformation. If the mechanical energy is made to rotate a dynamo the latter may deliver only (say) 90 per cent. of the E units that we expect from the equation $M = E$. The remainder can be (partially) traced as heat energy which is due to the friction, etc., of the imperfect mechanism of transformation.

(*d*) If we have C units of chemical energy in the form of coal which can unite with the oxygen of the air and burn we can cause *all* this chemical energy to transform into heat $= Q$. Now from (*b*) above this heat, Q is equivalent to M units of mechanical energy, but no mechanism enables us to effect this transformation. If we burn the coal in the furnace of a steam boiler and couple this to an engine we do obtain mechanical energy from heat, but we may obtain only about 10 per cent. of M. All the rest of the chemical energy of the coal transforms into heat.

Such examples can be multiplied. They show that

(*i*) Energy which can be made to transform passes wholly into heat; or

(*ii*) if it can be made to transform into some other energy-form some of it does not do so but transforms into heat;

(*iii*) and either all of the heat so transformed, or some of it, cannot be made to undergo any further transformation: that is, it becomes unavailable for further physical changes, or transformations.

and, therefore, the equivalence $M = Q$ is true in one sense $\overrightarrow{M = Q}$, but it is not true in the other sense $\overrightarrow{Q = M}$. This statement holds good for human experience, "so far as it goes." It means that in all known physical processes some of the involved available energy that transforms, or "keeps things going," is actually expended and, so far as our power goes, is annihilated or disappears. *Or* physical causality is continually being lost in the universe, as we know it.

22*e*. ENTROPY. The precise statement of the above matters is contained in the mathematical function called entropy. We consider the flow of heat. Let a system of things have a certain quantity of heat energy $= Q$. This heat will only flow, *of itself*, into another system of things if this latter system is at a lower temperature than the former one. (Obviously, for instance, the heat of a coal fire flows into, or warms up, a cold room.)

We say that the entropy of the first system is $\frac{Q}{T^\circ}$ (where T° is the absolute temperature, that is, ordinary Centigrade temperatures $+ 273^\circ$). Let Q units of heat flow from this system, then, the latter loses $\frac{Q}{T^\circ}$ entropy. But the second system, which is at a lower temperature than the first one, receives the heat that flows (if it were not at a lower temperature heat would not flow of itself). The temperature of this latter system is T°_2. Therefore it gains $\frac{Q}{T^\circ_2}$ entropy: and the Q's being the same, while T°_2 is less than T°, the entropy, $\frac{Q}{T^\circ_2}$, is greater than $\frac{Q}{T^\circ}$. And, therefore, entropy increases when heat flows, or is transformed in any actual way known to us.

The energy that propels a steamship is that represented by the fuel. This fuel is burned so that heat at, say, 1,000° C. is continually being generated in the furnaces and as continually flowing away. Actually some of it transforms into the mechanical energy of the engines, but whatever happens in the paths of the transferences and transformations of the heat the final phase is the same: heat, at (say) approximately 15° C. enters the ocean and atmosphere. So we have the result, for any small quantity of the heat that flows away from the furnace into, say, the ocean—

$$\textit{Initial entropy} = \frac{Q}{1000^\circ + 273^\circ} + C;$$

(*C* being a constant of unknown value.)

$$\textit{Final entropy} = \frac{Q}{15^\circ + 273^\circ} + C;$$

and, obviously the entropy associated with *Q* has increased.]

22*f*. DISSIPATED ENERGY. That quantity of energy represented by the burned fuel still exists. But now it is dissipated, and tends further to be dissipated, throughout the ocean, the atmosphere and cosmic space. It cannot be utilized (that is, by human control) and so it has become unavailable (*for human purposes*). It is energy that has become disorganized. In the ocean are immense reservoirs of heat-energy that man cannot utilize. It is quite conceivable that organisms of sizes approximate to those of molecules (endowed, as Clerk Maxwell says, with powers that are finite) might utilize this energy of low-temperature, disorganized heat and it is possible that micro-organisms may utilize it.

But macroscopic organisms, such as man, do not use energy that has been dissipated, or degraded, in the above sense. In all transformations that proceed in the course of organic functioning dissipation occurs. It is true that the tendency of plant metabolism *is to retard* the process of dissipation, but it is also true that in all metabolic processes dissipation ultimately occurs, even though it is retarded in some cases.

22*a*. IRREVERSIBLE ENERGY-TRANSFORMATIONS. Thus entropy increases in all physical changes known to us—

The Entropy of the Universe tends towards a maximum value. That means that physical changes occur in one direction—in

that direction in which entropy increases. It is not possible so to bring about a universal physical change in which entropy decreases. We can observe that water flows, of itself, from higher to lower levels (dissipating energy by friction as it does so). We can cause water to flow from lower to higher levels, by pumping it through pipes against a head of water, but in such a case we set up a coupled transformation, connecting the natural physical change with an artificial one. Then the gain in potential energy obtained by raising the water to a higher level is less than the quantity of energy dissipated in the pumping. Or we can cause heat to flow from the atmosphere of a cold-storage room to a reservoir of compressed air by the operations of compression ; or we can make heat flow from cold compressed ammonia gas (in a refrigeration plant) into the warmer atmosphere. But in such cases extraneous energy is again degraded.

So all energy-transformations occur in one way (ultimately)—in such a way that universal available energy is (from our point of view) expended irretrievably.

II. THE ANIMAL ACTION-SYSTEMS

According to the structural bodily plans that have been evolved so the action-systems differ : Thus we have the familiar pedal locomotory actions of, say, the mammals, the creeping locomotions of the snail, the ciliary movements of infusoria, etc.

23. *ON PEDAL LOCOMOTION AND ASSOCIATED ACTIONS*

Bi-Pedal locomotion is exhibited by man and some other Primate mammals and by birds. The motile appendages are limbs articulated with the body and jointed in themselves, thus the human leg with thigh, shin, ankle and pedal phalanges, all articulating with each other and provided with appropriate musculatures so that the limb has freedom of motion in all three dimensions of space. The terminal parts of the limb can exercise gripping action on the ground. The limb moves mainly as a pendulum, its pivot being the articulation with the pelvis and rapidity of movement is dependent, to some extent, upon the pendular length. Varying methods of articulation, and varying fusions of the skeletal parts (as in the " ankle " parts of the bird leg) modify the freedom of movement of the whole limb ; thus

the clutching movements of the toes of the birds. There is exact co-ordination of the right and left limbs.

Quadrupedal locomotion is exhibited by most mammals ; by most reptiles and many amphibia. There are four limbs, in two pairs. Fore and hind limbs act similarly (except as indicated below) and there is co-ordination between anterior and posterior pairs. Individually the limbs act much as in bipedal locomotion.

Multipedal locomotion is exhibited by many insects, crustacea, spiders, mites, worms, etc. In such cases the animal body is clearly segmental and each segment typically carries a pair of appendages. There may be anything from three to several dozen pairs of appendages. In the arthropods the latter are jointed and in these animals the motions of the " walking legs " are essentially similar to those of the quadruped mammals—that is from a mechanical point of view. Complete co-ordination is implied when there are many pairs of appendages.

Flight. In the cases of the birds, the mammals and the extinct flying reptiles the organs of flight are morphologically similar to the limbs of the quadruped. In the birds the fore limb is feathered ; in the mammals that fly (the bats) a light membrane is stretched between the fore and hind limbs and the body, and in the flying reptiles the membrane was stretched between the digits. In the insects the one or two pairs of wings are special appendages, morphologically different from the wings of birds and mammals. The wings are air-planes used in gliding (in the cases of the large birds) and, of course, as propellers also. They beat on the air with rapid oscillatory motions in the cases of the small birds and insects. In flying animals there are marked modifications of the other parts of the body. Thus the hollow and light bones of the bird, the shape of the body and the high efficiency of the respiratory organs.

Swimming. Most kinds of animals swim in water, either instinctively or by trial. In mammals, reptiles and amphibia the swimming organs are the limbs, used so as to propel the body in water. The birds rather paddle with the hind limbs, floating high out of the water and also diving. The fishes use the paired fins (which are morphologically similar to the limbs of mammals), but these organs are relatively inefficient compared with the tail : the median fins certainly, and the paired fins to some extent, act

as rudders and balancing organs. They are water-planes in the mechanical sense. *Swimmerets*, *parapodia*, etc., are bodily segmental appendages in crustacea, worms, etc., which belong to the same general series that we are regarding as "pedal." Their actions are those of paddles.

23*a*. Parts and Actions Associated with Pedal Organs. In all animals that move pedally the limbs or appendages are modified for other actions. The hands of man, the paws of the cats, or the hooves of horses and cattle, are examples of limbs used for "manufacture," aggression and defence. Among the arthropods the appendages are nearly always modified in groups: thus the antennæ and eyes of the lobster (sensory appendages); the mouth appendages which grasp and masticate food; the great claws (aggression)—the walking legs and swimmerets (abdominal appendages) are locomotory, but some of the latter may be copulatory.

Similar modifications of the appendages occur in the insects and worms.

24. *ON OTHER MODES OF LOCOMOTION*

A great part of the animal kingdom thus moves on limbs and other appendages, articulated on the body and performing rhythmic dragging, driving, or gliding motions on rigid surfaces, in air or in water. There are many other kinds of locomotion.

24*a*. Saltatory Mechanisms. Appendages may be used for locomotion by jumps—those of the flea, for instance. The whole abdomen of the shrimps, prawns and lobsters can violently flex (or bend) and the action, by reason of the grip on the water exerted by the telson (or tail) causes these animals to make backward bounds. The saltatory movements of many crustaceans (sand hoppers) appear to be made by violent flexions of the whole body. Some marine molluscs (the scallop, *Pecten*) bound in quite another way: the shell cavity is filled with water while the valves are widely open. Then folds of the mantle partially close the shell margins except in one place and the adductor muscle quickly closes the valves. The outrush of water from the shell cavity then causes the animal to bound backwards.

24*b*. Crawling Movements. Very many animals crawl slowly on rigid surfaces—the ground, rocks, the sea bottom, etc.

There are various mechanisms : (1) the segments of the earthworm are armed with spines placed like paired appendages : these catch on the ground or sand and rhythmic contractions and relaxations of the body drag the animal along—even in a burrow in soil ; (2) the body (as in the limpet, or common snail) has a broad, fleshy base, or " foot." This adheres to, say, the surface of a stone, or the ground, or some plant stem, leaves, etc. Rhythmic contractions and relaxations of the muscles of the foot drag the animal along ; (3) Echinoderms (starfishes, sea urchins, etc.) have the lower, or all the bodily surface covered by numbers of " tube-feet." These are hollow tubes provided with a kind of piston-sucker mechanism and they are full of liquid (mainly sea water). This is forced into or withdrawn from the tube-feet, actuating the sucker and extending or contracting the tube-feet. The latter adhere, in groups, to the surface on which the animal crawls, and the whole body is thus pulled along. Very complex and movement-groups of the tube-feet occur and complex and powerful movements of the body result—for instance, the starfish is able to pull open the valves of an oyster, right itself if turned upside-down, and so on.

24*c*. Rocket-Propulsion.—The Cephalopods, which may be very large and most predatory animals (some giant cuttle-fishes are competent to fight a sperm-whale), move about in two ways : (1) the " arms," or tentacles, have rows of suckers which can adhere with great force to some surface. These tentacles are strongly muscular and so the animal can grip, transport and crush other animals to which its tentacles are applied ; (2) there is a " mantle-cavity " in the body and this can be made to close. The cavity is filled with water and the muscles of the body violently contract so as to expel the contained water through a spout, or " siphon." The reaction produced by this expulsion makes the animal bound backwards. Somewhat analogous to this are the swimming movements of the medusoid Jelly-fishes.

24*d*. Ciliary Movements. This is the main mode of locomotion, and of general action, of most of the smaller, microscopic animals. (Many Protozoa, such as *Amœba*, crawl on rigid surfaces by " pseudopodial " actions) but most micro-organisms swim. The surface of the body is covered with minute, hair-like organs called *cilia*. A cilium " lashes," being flexed quickly and thus gripping on the water and pulling the animal along in the direction

of the lash. The cilium then recovers, or extends more slowly. Even in the small, microscopic protozoa there are great numbers of cilia and these are suitably arranged and lash in co-ordination. Extraordinary variety of movements, involving most complex co-ordinations of the cilia, occur and the complexity of this mode of movement cannot be much less simple (if at all) than the movements of the body and limbs of a mammal.

Ciliary movement is common in almost all groups of animals, in respiratory, cleansing and other movements. Thus the water currents into and out from the mantle cavity of such an animal as the mussel, or oyster, is maintained by cilia and even in man ciliary motions occur in the trachea, removing mucus, etc., into the mouth. In many animals the movements of food matter through the alimentary canal are maintained by cilia.

24*e*. Flagellate Movements. Each cell in the sponge has a motile, hair-like organ, a flagellum, or large cilium. The lashing of these establishes the incurrent and excurrent water movements. Hosts of protozoa and algal spores swim by the lashing of one or more flagella.

The writhing motions of the bodies of spirochætes, or the motions of spermatozoa are analogous. The whole spirochæte, or the tail of the spermatozoon writhes (like the tail of a tadpole or the whole body of an eel).

Many bacteria (minute as they are) are provided with groups of flagella and move by the lashing of these organs.

These are examples of action-mechanisms. In each there is a complex arrangement of motile parts—limbs, appendages, tendons, bones, muscles—all controlled by peripheral and central nervous organs and sensory parts *or* systems of suckers, tube-feet, etc., also under sensory and nervous control, *or* systems of cilia which do not have any nervous parts associated with them. In all cases every such mechanism has a general structural plan and it is capable of a certain variety of modes and amplitudes of movements. These modes of movement can be varied, by the method of trial and error, and by the experience of the animal, but the possible varieties and amplitudes are, of course, limited by the structural plans that have been evolved.

So far as we can see, all action-systems are actuated by muscles, or by ciliary and flagellate parts, which apply forces in some way

similar to those of the muscle-fibres. Little that is exact is known as to the nature of ciliary movements and much more is known about the muscle-fibre.

25. *ON THE NATURE OF MUSCULAR CONTRACTION*

A muscle, however it is disposed, always has its tendinous extremities attached to parts that are relatively fixed on the one hand, and " relatively movable," on the other. Thus the biceps muscle of the human arm " originates " in tendons attached to the humerus and this is the " relatively fixed " part. The other end of the muscle is " inserted " into the ulna and this is the " relatively movable " part. In all states the muscle is in a condition of slight tension (or " tonus "), but when it is going to act the tension between its two tendons suddenly increases and forces are applied to the parts into which these tendons are attached. One part (the humerus, in the above example) is relatively fixed, being held so by the tensions of other muscles, but the other part (the ulna) is free to move. We say that contraction of the biceps flexes the arm—that is, bends the forearm on the upper arm, via the elbow-joint.

25*a*. Structure of a Muscle. The essential parts are muscle-cells, which are short fibres, say from one-half to over an inch in length. Each fibre is bounded by a sheath and all the sheaths adhere to each other and are continuous with the tendons. The muscle-fibres are all colinear with each other. An artery carries blood to the muscle and it breaks up into arterioles and capillaries that ramify between the fibres. Blood thus flows through the capillaries and its liquid part passes through the capillary wall and fills up chinks between the muscle-fibres. A vein carries away spent blood from the muscle. Nerves go and come from the muscle. Lymphatic vessels are also connected with the apparatus.

25*b*. The Mechanism of a Muscle Contraction. The (motor) nerve that goes to the muscle breaks up into fine fibrils and one fibril goes to each muscle-fibre, where it terminates in a structure called the motor-plate. When a nervous impulse passes along the nerve into the muscle the latter contracts. Nervous impulses are momentary ones, so that the effect of one will be that the muscle momentarily twitches. A single nervous

impulse, however, seldom or never passes into a muscle: what the latter receives is a rapid succession of such and therefore the muscle passes into more or less sustained twitches, which blend into a contraction.

A nervous impulse is "all or nothing" and presumably the associated contraction of a muscle-fibre is also all or nothing. But the muscle contraction can be graduated according to the action that is to be performed: Therefore some or all of the fibres do not contract, the "strength" of the muscle-pull being proportional to the number of fibres that contract. Why this is so is obscure, but there are probably "quanta" of nervous impulse.

25*c*. THE ENERGY-TRANSFORMATIONS IN A MUSCULAR CONTRACTION. We consider only one fibre: when it is stimulated by a single nervous impulse its tension increases. If one or both of the parts to which the ends of the fibre are attached are free to move, then the tense fibre applies force to one or other of these parts, which thereupon move.

The muscle-fibre consists of ultimate parts, in the physical sense, and these parts are the fibrils, or sarcostyles, or they may be a series of fibrils continuous with the nerve endings in the motor-plate (the precise structure is not yet known without doubt). When the state of tension is initiated by the nervous impulse it may be that the sarcostyles tend to thicken transversely and so become tense, or the ultimate fibrils may simply *writhe*.

The muscle-fibre is "protoplasmic," but it contains some carbohydrate substance in a highly reactive condition and this substance has potential (chemical) energy. When the nervous impulse enters the fibre the carbohydrate undergoes sudden disintegration with the result that lactic acid is formed. Lactic acid has less available energy than the original carbohydrate and the balance of energy thus set free goes to raise the tension of the fibre (or the ultimate parts of the latter) that is, potential chemical energy transforms into the potential energy of the increased tension of the fibre. The transformation is complete, that is, the ratio

$$\frac{\text{energy of tension}}{\text{potential chemical energy set free}} = 1$$

If now the ends of the fibre are free to move they apply forces. The fibre shortens, thus doing work. It then returns to its original state until another nervous impulse enters it and the series

of events is repeated. Ultimately the muscle-fibre will refuse to respond unless the supply of carbohydrate and oxygen are renewed.

25*d*. OXIDATION IN THE MUSCLE-FIBRE. As the fibre continues to contract lactic acid accumulates in it. But the fibre continually receives oxygen from the blood and thus (*via* the agencies of oxidases—see Section 28*c*) the lactic acid is converted into CO_2 and OH_2. These latter substances are removed in the venous blood and eliminated from the body. But in the oxidation of lactic acid available energy is produced (for that of CO_2 and OH_2 is much less than that of lactic acid). Some of this energy coming from the oxidation of lactic acid restores that part of the carbohydrate that has supplied the energy of tension to its original reactive state. The rest of the energy of the oxidation transforms into heat. Ultimately, of course, the quantity of carbohydrate decreases and must be renewed.

25*e*. THE CONTRACTILE MUSCLE-FIBRE IS NOT A THERMODYNAMIC MECHANISM. A steam, or internal-combustion engine is a thermodynamic mechanism. In the former heat enters the cylinders, expands the steam and actuates the engine. Heat leaves the engine *via* the condenser water. More heat enters the engine in the steam than leaves it in the condenser water and the balance of heat energy transforms into the kinetic energy of the moving parts of the engine. There are two temperatures : T_2, which is that of the steam and T_1 which is that of the condenser water and $T_2 > T_1$. The greater is the difference $T_2 - T_1$, the greater is the efficiency of the engine (so an internal-combustion engine is more efficient than a steam-engine).

But if there is any such temperature-difference between the muscle which is more tense and that which is less tense it must be very small and so the muscle mechanism must be very inefficient—*if it is a thermodynamic mechanism*. But the muscle mechanism is highly efficient and therefore it cannot be a thermodynamic mechanism.

25*f*. THE MOTIVE FORCE OF MUSCULAR ACTIVITY DEPENDS ULTIMATELY ON THE OXIDATION OF CARBOHYDRATE MATERIAL. This must be obvious since the muscle carbohydrate disintegrates partially into lactic acid and the latter is removed by oxidation. The muscle supply of carbohydrate diminishes and must be

renewed. Therefore the functioning muscle must continually receive both carbohydrate and oxygen from the blood that flows through it.

III. THE ORGANS OF THE ENERGIZING SYSTEM

The action-systems of the animal body expend energy. Body, limbs, etc., all move against friction. Further, the organs that are concerned in the processes of organic functioning themselves move : the heart and arteries expand and contract, the lungs dilate and contract ; the walls of the alimentary canal exhibit peristaltic contractions and so on. Finally, the tissues of the body may generate heat.

Thus organic behaviour is accompanied—and enabled—by the dissipation of energy and so available energy must continually enter the body—to become unavailable in the course of behaviour.

The sources of this available energy are the nutritive materials taken in and the oxygen that is used in respiration. Ultimately all available energy used (or expended) in the organism, whether animal or vegetable, comes from the oxidation of materials derived from those other materials that are taken into the body.

26. *ON THE MATERIAL SOURCES OF ENERGY*

These are oxygen and the food substances (or the raw materials of the food substances). In the meantime we consider only the food substances.

26*a*. The Kinds of Materials taken into the Body.

(*i*) *By the typical plant organism.* Water, taken in by the root hairs from the medium in which the plant lives ;

Carbon Dioxide, taken in by the stomata of the green tissues ;

Compounds of Nitrogen, such as ammonia and its salts, nitric and nitrous acids and their salts ; other inorganic N-compounds ; these are dissolved in the intaken water ;

Mineral Salts, alkaline chlorides, carbonates, phosphates, etc., salts of iron, magnesium, manganese, etc. ; sulphates ; silica, etc. : these also are contained in the intaken water.

(*ii*) *By the typical animal organism.* The tissues of animals and plants : proteins, fats and oils, carbohydrates (perhaps also the cleavage-products of these substances) ; Water ;

Mineral Salts, as in vegetable organisms : these are contained in the other food-materials, or are dissolved in the intaken water.

(*iii*) *By atypical animals and plants.* Organic juices resulting from the chemical or bacterial decompositions of "organic matter."

27. *ON THE MODES OF INTAKE OF FOOD MATERIALS*

Here we consider merely the different ways in which food materials are taken into the organic body : presently we shall discuss the chemical and energetic transformations undergone by these materials.

27*a*. The Holophytic Mode. This is the completely, or typically plant way. The intaken materials are water, carbon dioxide and some mineral salts. The water is absorbed from the soil, or from the sea, etc., in the cases of aquatic plants. The mineral substances are contained in solution in this water. The latter is transported in the vessels of the plant tissues and comes into relation with CO_2 in the tissues underlying the green leaves, etc. The CO_2 is taken into the latter tissues through the pores (called stomata) in the green tissues.

At the same time solar radiation is absorbed by the general green surface of the plant. This gives the available energy that is required for the syntheses of carbohydrate, proteins and oils that are carried out on the raw materials taken in.

27*b*. The Holozoic Mode. This is the typical and completely animal mode of intake. The animal *captures* its food, which consists of the living or dead tissues of other animals or plants. It may capture and ingest the whole animal or plant organisms or it may dissect the latter, chew, gnaw, etc., parts and reject other parts. Or it may establish by ciliary action (sponges, molluscs, etc.) currents of water in which the food organisms are contained and it may filter this water in order to separate out the edible solid organisms ; which are then taken into the stomach.

Animals may be exclusively carnivorous or herbivorous, or omnivorous, but these are only acquired and non-essential differences. The food organisms, in all cases, are composed of proteins, fats, oils and carbohydrates and although there are well-marked vegetable proteins, etc., which are not quite the same

as the animal substances, yet on digestion plant and animal proteins, etc., give much the same cleavage products.

27*c*. The Saprozoic and Saprophytic Modes. Many animals (tapeworms and other parasites) live in the bodies of other animals. These internal parasites may have no trace of an alimentary canal and may simply absorb nutriment from the blood, lymph, or intestinal, or peritoneal fluids in which they are placed. The whole external surface of the parasite may be such an absorbent organ. It is probable that molluscs, etc., may also absorb dissolved organic matter contained in the water currents that flow through their mantle cavities. Deep sea fishes, etc., eat the ooze that lies on the ocean bottom ; this ooze is supposed to consist partly of the decomposing bodies of minute organisms that live in the water of the ocean near the surface. Infusoria and other protists live in " infusions," or liquids containing soluble organic matter.

There are analogous plant organisms feeding in the same essential way. In all cases what the saprozoic or saprophytic organism feeds on is soluble organic matter absorbed *via* the skin, gills or other external surfaces, or even by the mucous membrane of the alimentary canal, as when a man drinks " Oxo," or " Bovril," or some such liquid food. In the wild state the soluble organic matter comes from the decomposition of plant and animal tissues.

27*d*. The Ambiguous Modes. The above distinctions are not absolutely general. (1) Insectivorous plants can capture and digest the bodies of insects although they also utilize CO_2 and OH_2 in the typical holophytic mode. (2) " Plant-animals " (some worms, the zooids of some corals and exceptional molluscs) have green, chlorophyll—containing cells (" symbiotic algæ ") in their tissues and the latter cells can utilize CO_2 and OH_2 while the animal can also feed in the typical holozoic mode. (3) Some animals (molluscs and sponges and perhaps worms) can live on dissolved organic matter while also capturing and ingesting food organisms.

27*e*. The Bacterial Modes (Bacteria may be regarded as among the very primitive plants). They may be thus classified —as regards nutrition :

(*i*) *The Prototrophic forms.*

(*a*) Nitrifying Bacteria. These can, with either no organic matter, or a bare minimal quantity, break down nitric into nitrous

acid, nitrous acid into ammonia, and ammonia into elementary nitrogen (the denitrifying bacteria), *or* they can use the elementary nitrogen of the atmosphere (nitrogen-fixing bacteria). Some species can use CO_2 and OH_2, synthesizing these into carbohydrate with only a trace of organic matter and *in the dark*.

(*b*) Sulphur and Iron Bacteria can use sulphuretted hydrogen and iron salts as the raw materials for assimilation. Possibly there are analogous carbon and silica bacteria.

(*c*) The Root-Bacteria of Leguminous Plants. These are symbiotic with the tissues of the roots of peas, beans, etc. They can use elementary nitrogen.

(*ii*) *The myxotrophic forms.*

These are all the ordinary bacteria that may live in the open, or in organic matter, or in the tissues of animals. They are responsible for the processes of putrefaction and fermentation of organic materials. They get their energy by breaking up such substances.

(*iii*) *The paratrophic forms.*

These are the obligatory parasites and they occur only in the tissues and fluids of living organisms. These fluids and tissues are their raw food substances.

28. *ON THE PRELIMINARY TRANSFORMATIONS OF THE INTAKEN MATERIALS*

First we consider briefly the typical plant modes (see also Section 35).

28*a*. Photosynthesis of Carbohydrates and Proteins. CO_2 is taken into the plant tissues *via* the stomata of the green surfaces (leaves) and water containing inorganic nitrogenous and other salts is taken in *via* the roots and is transported to the tissues adjacent to the green surfaces. Here the CO_2 and OH_2, plus the energy of sunlight, combine to form sugar-like materials which, almost immediately, become further chemically transformed and are deposited in the leaf-tissues as sugar and starch granules.

At the same time simple proteins are synthesized from the sugar thus formed and the nitrogenous materials which were absorbed *via* the roots. These also are, at first, stored. This, in the case of starch formation, is carbon-assimilation. In the bacteria there are analogous processes of sulphur—and iron—assimilation.

28*b*. The Digestive Processes in Animals. First there may be the mechanical processes of mastication and deglutination: the food materials are disintegrated, mixed with water, and brought into the mouth, stomach, intestinal canal, etc., where they become mixed with the digestive enzymes.

28*c*. Enzymes. Very many of the chemical processes that occur in animals are initiated, controlled and accelerated by enzymes. These we conceive to be chemical substances that are elaborated in the glands and other bodily tissues. They act in much the same ways as the *catalysts* that have long been known in inorganic chemistry. Thus the inversion of cane sugar proceeds rapidly when its solution contains a little mineral acid; oxygen and coal gas can be made to combine when they are made to impinge on a tiny piece of platinum black; unsaturated fats and oils take up hydrogen, in certain conditions and in the presence of some nickel oxide; and so on. Analogous effects are such as this: perfectly dry chlorine and hydrogen do not combine, but do so quickly when the gases contain a trace of water vapour. In most cases a catalyst accelerates a chemical reaction that is possible in certain conditions but, in those conditions proceeds slowly, or "infinitely slowly."

By analogy enzymes are chemical substances, but no enzyme has ever been prepared in a pure state: it is always an extract from the tissue that has enzymatic qualities that is called an enzyme. It is usually a system rather than a single substance. Thus the pancreas secretes pancreatic juice and one active principle of this is *trypsinogen* which is the precursor of *trypsin*. But trypsin has no enzymatic qualities until it is "activated" by a substance secreted in the intestine called *enterokinase*. And there are analogous phenomena in the cases of other enzymes.

The digestive juices are active because they contain enzymes. The food materials ingested are complex in composition and usually they contain parts that are incapable of serving for nutrition. The various enzymes in the alimentary canal act on the raw food materials, some dealing with the proteins, others with the carbohydrates and others again with the fats. The undigested residues may be further disintegrated by bacterial action in the intestine and the final inutilizable products are expelled from the latter.

It is to be noted that the following account refers chiefly

to the higher mammals. But essentially the same processes can be said to occur in all animals having an alimentary canal and even in the cœlenterates and protists analogous enzymatic activities proceed. Of course the enzymes themselves are not quite the same in all animal forms. Thus the herbivores digest cellulose to an extent that does not characterize the digestive processes of the carnivores.

Digestion in the mouth. The digestive fluid is the saliva, which contains much mucin. It makes the " bolus " of masticated food which is swallowed. But it contains the *amylase* ptyalin. This converts starchy substances into soluble sugars, mainly maltose.

Digestion in the stomach. The fluid is the gastric juice, which contains about one-third per cent. of hydrochloric acid and the *protease* pepsin. There is a substance called pepsinogen in the mucous membrane of the stomach-wall and this is set free, in some way, by the action of CO_2. The pepsin acts on the emulsified fats to some extent (thus it contains a *lipase*), but mainly it converts proteins into " acid-albumen," proteoses, albumoses and peptones. It may (to a limited extent) split up the latter substances into amino-acids. It does not digest nucleins.

Digestion in the small intestine. The active fluids are pancreatic juice, intestinal juices and bile. The pancreatic juice contains a lipase called steapsin, an amylase called *amylopsin* and a protease called trypsin. The trypsin has a precursor, trypsinogen, and this is activated by the *enterokinase* of the duodenum.

Steapsin splits up fats into the constituent fatty acids and glycerol. Amylopsin dissolves starchy substances by converting them into maltose and other sugars. Trypsin does much the same things that pepsin does but carries the transformation of proteins further. Finally, in the intestine the peptides, etc., that have been formed by the action of pepsin become largely split up into amino-acids.

The bile-salts emulsify neutral fats, which, in this state, are more readily attacked by the amylase of the pancreatic juice.

The bacteria of the large intestine. Incredibly great numbers of *Bacilli* (*B. coli* is the type) live in the large intestine of mammals (and in corresponding parts of the alimentary canals of other vertebrates). They " deaminize " amino-acids, that is split off ammonia. Thus " proteid fragments " (such as leucine, tyrosine,

etc.), amino-bodies, offensively smelling ptomaines, etc., are formed at the latter end of the bowel. The fæces consist largely of bacteria, undigested food materials, protein fragments, etc.

Digestion in general. The foodstuffs, bulky in consistency and heterogeneous in constitution, become triturated in the mouth, œsophagus, stomach, etc., and are then subjected to chemical disintegrations by the agencies of enzymes. First their significant constituents—the proteins, fats and carbohydrates, are brought into solution :

the proteins as peptides, peptones, etc., and finally as amino-acids ;

the fats as fatty acids and glycerol ;

the carbohydrates as lævulose, glucose, maltose, galactose, etc., and these reduced products—the amino-acids, the fatty acids, the glycerol and the soluble sugars, are transformed foodstuffs ready to go into circulation.

29. *ON THE ABSORPTION AND CIRCULATION OF THE ELABORATED FOOD MATERIALS*

The heterogeneous contents of the small intestine are called *chyme.* Simultaneously with the formation of this mixture its absorption begins. The amino-acids and the soluble sugars are directly absorbed, passing through the inner wall of the intestine, and the thin walls of the capillaries, into the blood-stream. The fatty acids and glycerol also pass through the intestinal mucosa, but in so doing they are again combined into neutral fats. The creamy liquid which is called chyle and which is seen, after a meal, in the lymphatic vessels of the intestinal wall consists characteristically of minute droplets of neutral, emulsified fats. It goes into the vessel (in man) called the thoracic duct and is finally emptied into the blood-stream. Thus the latter is loaded, after every meal, with the proximate food substances, *amino-acids, carbohydrates as sugars* and *emulsified neutral fats.*

And it is from these substances that the energy-requirements of the animal body are met. Also the growth and repair of tissues are built up upon them. In the reproducing and pregnant animals they supply the materials from which ova and spermatozoa and the embryonic developing tissues are formed.

29*a*. The Circulation, throughout the Body, of the Proximate Food Substances. Generally, in the higher animals,

the blood coming from the intestine and going to the general circulation first passes through the liver, then, *via* the great veins, it reaches the heart. In all the higher animals the circulatory system has the same essential plan of structure : from the heart blood is propelled, through arterial vessels, to the respiratory organs, gills or lungs. There it takes up oxygen and eliminates CO_2. The circulation to the respiratory organs may form part of a single scheme, or it may be part of a double scheme.

In the Mammal. In whatever precise ways these purely hydraulic mechanisms are disposed the termini of the blood-stream are the living, functioning tissues. All these, whether muscles, or glands, or brain, etc., are permeated, in the minute parts, by a network of capillary vessels which distribute blood to them. Between the tissue-cells are lymph channels, chinks, irregular passages of obscure forms, etc., and the liquid part of the blood—the plasma—passes through the capillary walls, flows through the interstices between the tissue elements, gives up to the latter food substances and oxygen and is finally collected again by lymph channels and returned to the general blood-vessels. It is in this way that the functioning, growing, or repairing tissues are " fed."

30. *ON THE ORGANS OF RESPIRATION*

Whatever be the precise structures of the organs indicated in section (12*c*) this is always the case :

(*i*) *There is a respiratory membrane.* In the air-breathing higher animal this is the epithelium that lines the air-sacs of the lungs. In the fish, or other water-breathing animal, it is the epithelium covering the gill-lamellæ, etc.

(*ii*) *One side of the membrane is exposed to the oxygen-containing medium—air or water.* On the other side is a dense network of capillary blood-vessels. Blood that is venous, or " spent " as regards its O-content, is circulated through this network.

(*iii*) *The blood contains an oxygen-carrier.* This is hæmoglobin, or some analogous substance. It may be contained in cells —the red blood-corpuscles—or it may be dissolved in the fluid blood.

(*iv*). *There is a gaseous interchange between the blood and the*

oxygen-containing medium. Oxygen at a relatively high tension in the O-medium passes through the respiratory membrane and through the walls of the capillary vessels to the O-carrier—where oxygen is at a relatively low tension. CO_2, at a relatively high tension in the fluid part of the blood passes through the capillary walls and the respiratory membrane to the respiratory medium (air or water) where it is at a relatively low tension.

Thus the blood that goes to its termini in the tissues carries oxygen as well as the proximate food substances. When it returns from the termini it carries back CO_2, to be passed out into the water or air.

We do not know the precise physical details of the respiratory gaseous interchanges—in spite of much research. Nevertheless, it is without doubt that all the details of these processes are strictly physical and chemical in the ordinary senses of these terms.

31. *ON ASSIMILATION*

Chemical analysis of the substances of the animal body shows that these are roughly as follows :

(*i*) The ubiquitous water of which all tissues contain, say, from 30 to 80 or so per cent.

(*ii*) *The skeletal matrices :* bone, shell, cartilage, chitin, hydrated silica, sclero-proteins (in horn, feathers, etc.).

(*iii*) *The structural "protoplasm,"* that is, the substances of the tissue-mechanisms—muscle substance, that of nerve, the substance of gland cells, connective tissue, etc. Protoplasm is not a single substance but a complex of proteins, lipins, etc.

(*iv*) *The reserves :* fat in adipose tissues ; glycogen, or other carbohydrate in the liver or muscles ; possibly the globulins and albumens of the blood.

It will be convenient (and adequate for the present purpose) to consider the structural protoplasm, the blood and the reserves as constituted by proteins, fats and carbohydrates.

These substances are not necessarily the same in different species of animals. Thus there are the differences between the fats of bacon, of beef and of mutton ; between the proteins of mutton, lean beef, cod, peas, cheese, etc. In all these cases the protein has the same general chemical structure, a complex of amino-acid " building stones," but the specific proteins are recognizably

different. And the differences between proteins follow, to some degree, the natural classification of animals: Thus the blood proteins of man are more like those of the anthropoid apes than they are like the proteins, say, of sheep and goats.

Thus although the food substances of (say) a man may be mammalian proteins and fats and vegetable carbohydrates, these proteins, fats and carbohydrates are not the same as the human proteins, fats and carbohydrates.

Nevertheless, all proteins can be chemically broken down into amino-acids (of which there are few compared with the proteins); all fats can be similarly broken down into fatty acids and glycerol; all carbohydrates can be hydrolyzed and otherwise changed so as to form a relatively small group of sugars. These disintegrations occur during the processes of digestion.

And since the human body (analysed as above) is not a complex of amino-acids, fatty acids, glycerol and sugars it follows that, after the digestion of the raw food substances, and their resolution into the amino and fatty acids, the glycerol and sugars, these latter substances must again be re-synthesized into the human proteins, fats and carbohydrates. *This is assimilation.*

31*a*. Chemical Assimilation. The assimilation is, in the first place, a chemical one—the proteins ingested, as the foods, *are made similar* to the proteins of the animals that eat those foods. The process was believed to be one effected by the same enzymes that effected the digestive changes. Thus the action of a catalyst is often reversible: for instance, amyl nitrite can be hydrolyzed by boiling with alcoholic potash, but at the same time the potassium nitrite will tend to be dissociated into potassium hydrate and into nitrous acid, which again forms an ester (amyl nitrite) with the amyl alcohol which was formed in the first phase of the reaction. So it was believed that the same lipase that split up the neutral fat in the intestine also recombined the fatty acid and glycerol into neutral fat in the intestinal mucosa, or in the lacteal vessels. This is not exactly the case, however, since the neutral fats that go into the blood-stream are not the same as those that were in the foods.

Therefore the enzymes cannot be strictly reversible ones.

The details of the chemical assimilations are not known. However the amino acids that pass into the blood-stream after digestion are again synthesized into proteins—in the liver and tissues to

which these substances are distributed. The fatty acids and glycerol are combined as fats in the intestinal wall. The soluble sugars are, in part, distributed to the tissues but go, in the main, to the liver where they are converted into glycogens.

31*b*. On Structural Assimilation. It is sometimes said that some bodily parts (the nerve-cells and fibres, the muscle-cells, etc.) are " alive " while other substances, the glycogen of the liver, the carbohydrate of the muscle-fibre, the neutral fat of adipose tissue, etc., are " not alive." But in the obvious difficulty of defining " living substance " the distinction suggested is not clear.

There is, however, some difference in a fundamental sense between the substance of the tissue-mechanism (say the sarcostyles of a muscle-fibre, regarded as contractile tissue) and the energy-yielding substances associated with the tissue-mechanism. (Say the carbohydrate in the muscle fibres that disintegrate and yield energy to set up the muscular tensions.) Also we think about the bodily fats, which are used up in starvation, as different in some deep sense from the connective tissue-cells in which the fats are " stored," or the matrices of bone and cartilage are not so obviously " vital " as the bone and cartilage cells that lay down these matrices. In some way " stored," or " reserve," or mechanical-supporting substances are different from, and subsidiary to, the tissue-mechanisms.

The latter are subject to waste and must be repaired. Also there is actual increase in their mass, in bodily growth. Therefore the materials that have been chemically assimilated must, to some extent, be structurally assimilated, or incorporated, or *incarnated* into the obviously functioning parts of the body.

So there is one kind of flesh of beasts and another of fowls and so on. The flesh, etc., that is eaten is broken down into its chemical parts from which some other kind of flesh can be constructed. The analytic changes are imperfectly known, but the synthetic ones, involving not only chemical transformations but also specific tectonic ones are certainly among the unsolved problems of physiology.

32. *ON THE ORGANS OF EXCRETION*

On the analogy of the heat-engine we expect various " products of combustion " to be eliminated from the animal body. Since

all bodily energy is ultimately derived from the oxidation of carbon and hydrogen we expect that CO_2 and OH_2 will be prominent constituents of the excretions.

32*a*. ORIGINS OF THE EXCRETED SUBSTANCES. The CO_2 and OH_2 come mainly from the oxidation of the lactic acid produced when the muscle-fibres pass into the state of tension. But CO_2 is produced in the activities of other tissue-elements—even from nerve-cells and nerve-fibres. There is also waste in all tissues that function: thus the numbers of "worn-out," red blood-corpuscles that are destroyed in the liver every second are very large, and so on. Nitrogenous residues come from such waste and also from the utilization of proteins as energy-sources.

32*b*. EXCRETORY PATHS. CO_2 is eliminated from the respiratory organ (see Section 30). The latter is the lung, gill, general integument, etc., but the physical process of excretion of CO_2 is probably essentially the same in all higher animals. Water is excreted *via* the kidneys, or renal organs in non-vertebrate animals, or from the respiratory organs, or from the skin in many terrestrial animals. Fæcal matters are to some extent excretions, as they consist of worn-out, essential intestinal bacteria, the pigments and other materials eliminated from the body in the bile that passes into the intestine from the liver, and of unabsorbed materials of foodstuffs.

32*c*. THE NITROGENOUS RESIDUES are eliminated *via* the kidneys or renal organs. They have a general chemical similarity, consisting of urea, uric acid, hippuric acid, etc. (see Section 73).

33. *ON ORGANS OF SPECIAL METABOLISM*

By "metabolism" is meant, in general, the chemical transformations undergone by the materials of the living organism. It includes, for instance, the disintegration of carbohydrate in the muscle-fibre and the oxidation of the resulting lactic acid. But there are organs where quite special changes occur and it will be convenient to consider these separately.

The liver is a metabolic organ that has many functions: it transforms sugars (from the intestinal blood) into glycogen, liberates and hydrolyzes glycogen into sugars which are discharged

into the blood-stream, deaminizes nitrogneous residues, eliminates the wasted blood corpuscles, etc.

The lymphatic glands have to do with the elaboration of lymph, intercept detrimental materials that get into the blood and so on.

The spleen is in the nature of a lymphatic organ.

The red marrow of the long bone cavities has to do with the elaboration of red blood-corpuscles.

The endocrine glands. These are the thyroid, the associated *parathyroids*, *the thymus*, the *pituitary* and *pineal* bodies, the *adrenal glands* and the *interstitial tissues of the gonads*. All of these are ductless glands and they make changes of some kind in the blood that flows through them.

Without doubt they elaborate definite chemical substances which then enter the general blood-stream and lead to changes in the functioning of various organs. Thus *thyroxin* is made in the thyroid and *adrenaline* in the adrenal organs. In the other cases the elaboration of some materials of great significance is inferred from the effects that operative interference with, or disease of the glands produce : also by analogy with the better-known organs—the thyroid and adrenals.

In the above section we refer particularly to the endocrine and other glands of man and the higher mammals. Analogous organs and functions exist in all animals, but their investigation is very incomplete.

33*a*. CHANGE OF FUNCTIONING. These organs afford good examples of the changes of functions that animal organs undergo in the course of evolution. In molluscs the " liver " is a digestive gland. In the primitive chordates the " thyroid " is the endostyle —an organ connected with the intake of food. In the lower reptiles the " pineal gland " is a median eye (in the physiology of Descartes it was regarded as the seat of the soul). In the unknown ancestors of the vertebrates part of the " pituitary gland " was part of the mouth. In the vertebrates the " adrenal organs " seem to have been connected, in some way, with the sympathetic nervous system. In Teleostean fishes the " kidney " is also a lymphatic gland.

While structure is very conservative in the animal kingdom the functioning of some structure changes in the course of evolution. This is a very general effect of the evolutionary process.

34. *ON CO-ORDINATION AND REGULATIONS OF FUNCTIONING*

It is convenient in exposition, and quite necessary in investigation to deal analytically with organs and modes of functioning and behaviour. Nevertheless, it is true to say that the animal body behaves and functions as one thing. Thus if an animal makes some violent exertion everything in its body participates in that activity. The muscles apply forces to the moving limbs and other parts ; the rate of beat of the heart increases ; the respiratory organs function more vigorously ; glycogen is discharged from the liver (or other reserves are mobilized) and so on.

34*a*. Integration of Functioning. The whole nervous system is an integrative organ, connecting together all parts and co-ordinating all activities. The blood-stream, which is a continuous fluid in all organs, receives excretory products from all and gives materials to all. The common framework of connective tissue that is everywhere in the body is not only a common mechanical structure but has, possibly, some chemical function and so on. Thus everything that happens anywhere affects, in some degree, everything else. Every bodily activity, though it is mainly expressed as some behaviour-pattern, involves many other neuro-muscular mechanisms than the characteristic one and the organic functioning which energizes the muscular activities involves most, or all, of the metabolic organs.

It necessarily involves oxidations of carbohydrates so that the muscle stores of those substances must be made good from the circulating blood. On the other hand, the latter becomes loaded with CO_2 which must be eliminated. In bodily activities the composition of the blood must tend continually to change, yet its constancy of composition and its reaction vary only within very narrow limits. This constancy is maintained by the functioning of the metabolic organs.

34*b*. Regulatory Mechanisms. Mainly these are nervous and muscular. They are automatic and the automatism may be regarded as the expression of a *need*—that of organic normality. Heat-regulation, for example, in the mammal depends largely on a nerve-muscle mechanism : the need is for a constant bodily temperature. Should this rise, the muscles in the walls of the arterioles of the skin dilate ; there is an increased blood flow just

where the heat of the blood-stream is the more easily conducted to the open air and so the exercising man feels warm—because he is losing heat through his skin. He also sweats more and this is because the secretion from the skin glands increases, since the blood flows more rapidly through these organs.

In violent bodily exertion CO_2 tends to accumulate in the blood. But there is a respiratory centre in the medulla and this is affected by the tension of CO_2 in the blood-stream—in this way: increased CO_2-tension stimulates the nerves that accelerate the respiratory movements—thus CO_2 in the blood is eliminated more rapidly than normal. Conversely decreased CO_2-tension retards the same muscular movements and the rate of gaseous interchange in the lungs is decreased. On the prolonged scale this regulation proceeds in the cases of hibernating mammals.

34*c*. CHEMICAL REGULATIONS. The secretion of pancreatic juice, for instance, appears to be regulated apart from nervous-muscular mechanisms. The entrance into the duodenum, from the stomach, of partially digested food materials appears to be accompanied by the elaboration of a substance called secretin. This goes into the blood-stream and stimulates the pancreas to secretion. Such substances are called *hormones*, and it is believed that they have a general rôle in chemical adjustments, and even in developmental processes.

The regulatory mechanisms are doubtless physico-chemical ones and the conception of automatic workings of such mechanisms is an easy one. Models can be devised and there are obvious mechanical analogues—in the throttle-gear of a steam, or gas engine, for instance. (But the evolution of the automatisms is not so easy to conceive, for the throttle-gear of a heat engine is *designed*.)

And all the fundamental problems involved in such automatic regulations are unsolved: we do not know in what physical or chemical ways CO_2 in the blood-stream affects the ganglionic cells of the respiratory centre so that the latter *now* sends out inhibitory impulses, and *again* acceleratory ones. And, of course, we do not know how, precisely, a nervous impulse entering a muscle-fibre can alter the state of tension of the latter. Yet this is the most common and fundamental of all physiological activities.

IV. THE ENERGETICS OF ORGANISMS

It is convenient to make the distinction between physico-chemical reactions that occur of themselves, and those that will only occur when they are *coupled* with other reactions that occur of themselves.

When a chemical reaction, say $2H_2 + O_2 = 2H_2O$, occurs of itself free or available energy is generated. Usually heat is produced. Such a reaction is, in cases where heat is generated, called *exothermic*. When a reaction, chemical or physico-chemical, occurs of itself, energy is dissipated and entropy increases.

Coal burns in an atmosphere containing oxygen and these reactions happen, $C + O_2 = CO_2$, $2H_2 + O_2 = 2H_2O$. But the CO_2 does not, of itself, combine with O to form a compound CO_3. Nor does H_2O combine with O, *of itself*, to form a compound H_2O_2.

But the *possible* reaction, $H_2O + O = H_2O_2$, *can* occur when this possibility is coupled with some other reaction in which free, or available, energy is produced. Then hydrogen peroxide is formed and the reaction is called an *endothermic* one.

35. *ON TYPICAL PLANT METABOLISM*

The characteristic chemical reactions occurring in the green plant are those leading to *carbon-assimilation*. Here we find that these chemical reactions occur :

$$CO_2 + OH_2 = \underset{\text{formaldehyde}}{H.CHO} + O_2$$

$$6H.CHO = \underset{\text{a carbohydrate.}}{C_6H_{12}O_6}$$

Now these reactions do not occur of themselves but only when the green plant is exposed to sunlight which contains radiation of high frequency. Usually this high-frequency radiation degrades, as when it falls on the ocean which is then heated, or suffers evaporation, which leads in the long run to the dissipation of heat. In this latter case energy is dissipated and entropy increases.

But when the high-frequency radiation is intercepted by the chlorophyll of the green plant, some of it does not degrade.

This energy is coupled with the system CO_2, OH_2 and so the formation of formaldehyde occurs. In the latter reaction two things are involved, (1) the possibility of the combination of CO_2 and OH_2 and (2) the available energy supplied by the degrading solar radiation. So we have the conspicuously endothermic reaction :

$$(1) \qquad \underset{\substack{\textit{Reactants that}\\ \text{have no available}\\ \text{energy}}}{CO_2 + OH_2} = \underset{\substack{\textit{Resultants that}\\ \text{have much available}\\ \text{energy}}}{H.CHO + O_2}$$

and the process—

$$(2) \quad \begin{matrix}\text{Solar radiation}\\ \text{of high frequency}\end{matrix} = \begin{matrix}\text{solar radiation}\\ \text{of low frequency}\end{matrix} + \begin{matrix}\text{available}\\ \text{energy.}\end{matrix}$$

The available energy represented in the right-hand side of the second equation accounts for the fact that the resultants in the first equation have more available energy than had the reactants. In their formation entropy *locally* decreases.

In analogous ways nitrogen-assimilation occurs in plants.

35*a*. Anabolic and Katabolic Processes. These plant assimilations are called *anabolic processes*. But in all plants other processes leading to mechanical effects, etc., occur. Thus a tree raises matter (its own substance) into the air against gravity ; its parts move, flowers may open or shut ; roots and tendrils move, climb, etc. ; water (the sap) is circulated ; transpiration of water occurs ; oxidations occur, etc. In these processes energy, in the available form, is expended and degrades. Their energy comes from reactions of the form

$$\underset{\text{reactants}}{C + O_2} = \underset{\text{resultant}}{CO_2} + \begin{matrix}\text{available}\\ \text{energy.}\end{matrix}$$

And the available energy so set free makes possible the effects mentioned. These latter processes are called *katabolic* ones. In them energy degrades and entropy increases.

But in plants, in general, the anabolic processes are greatly in excess of the katabolic ones. So in plants, in general, entropy locally increases. Regarding plants as parts of the universe we conclude that *their effect is to retard entropy-growth* by preventing the complete dissipation of solar energy. The general results of their activities is that available energy in the forms of plant

tissues, grains, seeds, woods, leaves, stalks, peat, lignite, coal, oil, etc., tends to accumulate on the earth.

35*b*. The Improbability of Coupled Energy-transformations. Coupled reactions occur:

(*a*) When living organisms (such as plants) unconsciously use solar radiation to effect reactions such as would not occur in their absence. (But most of the solar radiation falling on the ocean, deserts, sands, rocks, etc., of the earth's surface is simply dissipated);

(*b*) Where experimenters, acting consciously and deliberately, couple together reactions and energies. But their total effect is infinitesimal relatively to the radiation that degrades of itself);

(*c*) At random, say, in the turmoil of energies involved in the ejection of volcanic materials, or in plutonic and metamorphic processes in the earth's crust, etc. (But such effects do not often occur, so far as we know, and not relatively to the extent to which dissipative effects occur.)

Therefore coupled reactions that delay universal entropy-increase do not often occur compared with those in which entropy-increase freely occurs—*or they are improbable.*

36. *ON TYPICAL ANIMAL METABOLISM*

The typical animal organism does not, so far as we know, assimilate carbon and nitrogen in the way the plant does, nor is it known to utilize solar radiation of high frequency as a source of energy. It can utilize solar radiation, when the latter has degraded into heat (low-frequency radiation) in that it "warms itself" in the sun. It cannot make use, as foodstuffs, of CO_2, OH_2, inorganic compounds of nitrogen, etc., in the way that the typical plant does.

The typical animal that is full grown and is not reproducing nourishes itself by ingesting proteins, fats and carbohydrates obtained as, or from, the tissues of living or dead animals and plants. It transforms these substances in its own body in such ways that they are ultimately chemically degraded into CO_2, OH_2, urea and other nitrogenous residues. The general course of the chemical transformations is one of oxidation and during them available energy is set free.

Proteins, fats and carbohydrate being oxidized	*give rise to*	$CO_2 + OH_2 +$ nitrogenous residues + available energy.

The available energy is mainly expended in the muscular motions of circulation of bodily fluids, respiration, etc., and of the muscular motions of the body and its members during the activities of behaviour. In these activities available energy dissipates. In general the activities of the fully-grown, non-reproductive typical animal are *katabolic ones.*

36*a*. Anabolic Processes in Animals. But when the animal is growing its foodstuffs are not merely oxidized, and so degraded, but are built up into new bodily tissues. And when it is reproducing the materials of the foodstuffs are converted also into the substances of eggs and spermatozoa, or (if it is a pregnant or nursing parent) into the materials of the embryonic tissues. So the processes are anabolic ones, to that extent.

In a plant population the tissues of the bodies may accumulate as vegetable débris, etc. (see above). But in an animal population there is no accumulation of the substances of the bodies, for when the latter die their tissues are resolved into CO_2, OH_2, inorganic nitrogenous salts, etc.—materials in which the energies have been dissipated. Therefore the general result of animal metabolism is to lead to energy-dissipation—or entropy-increase.

36*b*. The Effects of Behaviour. The energetic effects of animal behaviour are indeterminate. Thus all the activities of a community of men might be given over to war and its preparation—in that case the energy of the population would simply be dissipated, in the energetic sense. Or the population might be a pastoral-agricultural one, in which case it might raise crops and cattle and so largely increase the quantities of available energy—and retard entropy-increase. And so with other animals.

In general the results of animal activity are to accelerate the dissipation of energy, that is to accelerate entropy-increase.

36*c*. The Animal Engine. In the heat engine (steam, gas, petrol) the kinetic energy comes from the oxidation of the fuel, which burns to CO_2 and OH_2. This is not directly the case with the animal engine, where part of the potential energy of

the foodstuffs transforms directly into kinetic muscular energy. But ultimately *all* the foodstuffs, except some small nitrogenous residues, transform, by oxidation, into CO_2 and OH_2. In inanimate and animate engines alike the *input* is food (fuel) and oxygen, and the *output* is kinetic energy of movement, heat and the waste substances.

36*d*. THE RÔLE OF BACTERIA. It is only in exceptional conditions that animal substances persist in nature (perhaps petroleum has had animal origin). In general putrefactive bacteria, with nitrifying species, reduce all proteins to CO_2, OH_2 and ultimately nitric acid, while fermentative bacteria reduce the fats and carbohydrates also to CO_2 and OH_2. Much plant substance is also disintegrated in such ways, but the celluloses and perhaps the vegetable oils tend to persist in geological time as peats, lignites, coal and perhaps petroleum.

37. *ON THE INTERDEPENDENCE OF PLANT, ANIMAL AND BACTERIAL ORGANISMS*

It is doubtful if plant organisms could continue indefinitely to inhabit an earth physically as it is at present but devoid of animal life. The tendency of plant metabolism is to fix CO_2 as fossil remains of the nature of coal, etc., and perhaps in limestone.

It is certain that animals, constituted as at present, could not continue long to inhabit an earth devoid of plant life. They are unable to utilize inorganic materials as the sources of energy, or of tissue-formation.

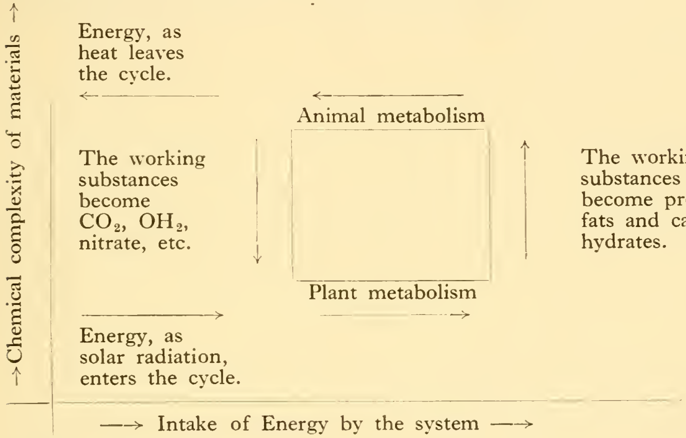
It is certain that very many forms of bacterial organisms can only exist as parasites on living plants and animals, or as saprophytes on plant and animal débris. It is doubtful (but perhaps it is possible) that some exceptional kinds of bacteria could continue to live on an earth physically as at present but devoid of plant and animal life.

37*a*. PRODUCERS AND CONSUMERS. Plants can make use of lifeless materials, building up the inorganic CO_2, OH_2 and inorganic nitrogenous and other salts into their tissue substances—in doing so they arrest the degrading solar radiation and find energy from this that enables them to carry out the chemical transformations noted above.

Plant organisms are therefore producers. Animals can only utilize the already built-up proteins, fats and carbohydrates. In their metabolism they oxidize and energetically degrade these materials—which they cannot themselves elaborate from inorganic sources. By reproduction animals can increase the mass of animal organisms and tissue-substances but, in general, the limit of reproductive increase is already attained.

37*b*. THE BACTERIAL-PLANT-ANIMAL METABOLISM IN ANALOGY WITH THE CARNOT CYCLE.

The working substances are O, C, N, H, S, P, etc.



This means :

(i) The working substances undergo cyclical changes ;

(ii) Plants absorb energy from sunlight and this energy becomes potential in the carbohydrates, etc., which are built up by the rearrangements, in more complex ways, of the working substances ; energy enters the cycle ;

(iii) Animals utilize these carbohydrates as food, oxidizing them to CO_2, OH_2, urea, etc. ; bacteria further break down the urea ; energy is dissipated and leaves the cycle.

(iv) The CO_2, OH_2, HNO_3, etc., are again used as sources of food by plants and the cycle begins again.

38. *ON THE LAWS OF CONSERVATION AND DISSIPATION IN ORGANISMS*

The experimental work is practically restricted to animals.

38*a*. FOOD VALUES. Small quantities of proteins, fats and

carbohydrates can be completely dried and then put into a bomb calorimeter and burned in oxygen. In this way their available energy, expressed as heat, can be found.

One gram of protein so burned gives	4·0	calories
,, ,, carbohydrate ,, ,,	4·0	,,
,, ,, fat ,, ,,	8·9	,,

(or figures very close to the above ones).

Then the different kinds of raw and cooked foods are analysed so as to give their percentages of dry protein, fat and carbohydrate. From these analyses, and the above calorific values, we can find the quantities of energy put into an animal, in the form of its food.

38*b*. THE INPUT AND OUTPUT OF ENERGY. Large calorimeters are used in the experiments. The calorimeter is really a small room, heat insulated and with perfectly controlled ventilation. The quantities of air entering it are accurately measured and the quantity of O_2, CO_2 and OH_2 leaving it are also measured. The excreta of the experimental animal are measured and analysed. The animal is usually a medical student who works, eats, excretes, sleeps, etc., for definite periods in the calorimeter. The work done, say by riding an experimental, fixed bicycle is recorded and so on. The animal, being in constant weight and in " nitrogenous equilibrium," takes in so much energy in the form of food, and gives out so much in the form of heat, mechanical work, heat and calorific energy of the excretions and so on. Thus an approximately accurate balance can be struck between the input and output of energy.

It has been found that the following quantities apply to the average man.

When sleeping he utilizes	1,500	calories per 24 hours.
,, lying down ,,	1,700	,, ,, ,, ,,
,, sitting ,, ,,	2,400	,, ,, ,, ,,
,, doing sedentary work ,,	2,400	,, ,, ,, ,,
,, doing heavy work ,,	4,000–6,000	,, ,, ,,

and so on. The different experiments made give results that are very much the same as those quoted above.

If, in a great many experiments, the energy taken in is compared with that given out the figures almost balance. Thus, for instance, *Energy input* 418,665 Cal. *Energy output* 416,634 Cal. *Therefore the laws of conservation of energy and matter apply to the*

organism with the strictness to which they apply to the inanimate system.

38*c*. QUALIFICATIONS OF THE ABOVE STATEMENT. Living phenomena that can be observed are (for instances): motions, quantities and natures of materials taking part in a reaction, velocity of a nervous impulse, frequency of nervous impulses, rate of flow of the blood, viscosity of muscle-substance, tension of a muscle, electric potentials developed by a muscle contraction, or a nervous impulse, oxygen inspired, CO_2 expired, reaction time, and so on.

There are also pleasure, pain, feeling, consciousness in general and so on. These are obvious life-phenomena for the experimenter and, irresistibly by analogy, for other men and women and animals.

Precise physiological results take the forms of equations such as that quoted above for the energy-balance. Such equations are (relatively to physical science) few in physiological investigations. In general an equation, such as we are now considering, takes the form

$$F = f(m, n, o)$$

F is some function of the variables, m, n, o, so that when m, n, o are given definite values, the form of the mathematical function enables us to find F in a perfectly definite way. (There are, of course, experimental errors which the physiologist can positively appraise.)

F must be of the same denominations, in a physical sense, as m, n, o. F, for instance, may be some quantity of heat energy expressed in calories, and so reducible to absolute units of energy; m, n, o may be quantities of heat, or electric potential, of mechanical work, of water synthesized, etc., and so also reducible to absolute units. Both sides of the equation must involve physical quantities which are fundamentally the same.

Now feelings, *consciousness*, *etc.*, *cannot be equated to mass*, *heat*, *electric potential*, etc. (and thus the well-known *relation* which connects increments of sensation with increments of stimulus is not an equation recognizable by mathematical physics).

Therefore obvious living phenomena may not always be put into mathematical-physical relations with obvious life-phenomena which *can* be given precise physical values.

The limits of measurement. Further, physiological measurements in the present state of science usually involve the use of the chemical balance, the thermometer, galvanometer, time-recording instruments, etc. So far as these are concerned, the quantities equated usually balance within certain limits of error. But in the physics of radiation much more minute quantities are now significant. Thus infinitesimal and hardly measurable quantities of electric energy impinge on the " grid " of a wireless valve and lead to large effects. Comparable with this are, quite certainly, hosts of life-phenomena—for instance, the occurrences in a nerve-synapse (see Section 41*a*).

So that the law of conservation is true for life-phenomena so far as gross chemico-physical measurements go.

Finally, the law of conservation is an *a priori* one : it is something that we postulate. No physical result can invalidate it (either in physics or in physiology). If precise measurements appeared to invalidate it we should merely look for, and find, new forms or phases of energy that would save the " law " (see Section 22*b*).

38*d*. The Law of Dissipation. This holds for the organism with all the strictness that it holds for inanimate systems. *In all life-processes some energy is dissipated and entropy increases.* The law expresses an inevitable, ultimate tendency and result : entropy always increases in every process which involves the whole universe. Every experimental, or scientifically localized, process does involve the whole universe, since the physicists' isolated physico-chemical system is only a convenient fiction. The experimenter, or the unconsciously acting organism, can cause entropy to decrease *locally*, but only by causing it to increase somewhere else outside the " isolated system."

The organism, and in particular man, can locally and temporally retard entropy-increase by processes of " sorting," control or direction. It is by reason of this sorting, or control, that the organism differs from the inanimate system.

38*e*. Modes, Forms and Phases of Energy. Lastly, there are no indications that particular forms, etc., of energy are exclusive to organisms. The visible phenomena of life, *so far as these are susceptible of receiving energetic expressions*, are expressed in energy ; forms that are the same as those we know in *inanimate* systems.

CHAPTER IV

ANIMAL BEHAVIOUR

By animal behaviour is meant the whole activities, with their meanings, of the organism regarded as a unitary thing. But it is convenient first to dissociate these activities in an arbitrary way. That has partially been done in Section 12*a*, where the *effector organs*, that is the system of limbs, appendages, teeth, claws, etc., were summarily described, and also in Sections 12, *b–e*, where the *energizing organs*, that is, those of alimentation, respiration, etc., were also described : these latter organs must be regarded as subserving the effector ones.

First, in this chapter, we consider the *organs of sensation and integration*, that is, the receptors, the peripheral nervous system and the nervous centres. Thus we complete the account of the *means of behaviour*. Next we take up the study of the purposes, and the grades of complexity of behaviouristic activity in the animal kingdom and lastly we have to consider behaviour in itself and apart from any analytical discussion of its nature. It is to be noted that throughout we restrict our study to animal organisms. Something of the nature of behaviour, as we think about it in animals, is also to be seen among plant organisms and, of course, in those Protista which we regard almost indifferently as either plant or animal. But the subject is one that applies almost entirely to the animal kingdom.

I. THE ORGANS OF THE "SENSORI-MOTOR" SYSTEM

These are the Receptors, or "sense-organs"; the afferent and efferent nerves, the central ganglia and the effector organs.

39. *ON THE RECEPTOR ORGANS*

The whole substance of the body of an animal is *irritable*, that is, it *responds* (changes, contracts, etc.) when it is *stimulated*

(that is, is exposed to some physical agency, touch, chemical action, heat, etc.).

Irritability is just a special case of physical inter-relationship among natural things: one billiard ball impinges on another and causes it to move; the rays of the sun heat up stones, or dry up the water of pools; a lightning flash may set dry timber afire and so on. In its immediate nature the stimulation of the irritable substance of an organism is no more than this.

The outer surface of the animal body is especially irritable and exhibits responses to simple contact with other bodies, to changes of temperature, to contact with specific chemical substances, to electric currents and charges, to light, etc. It is proper to think of the whole integument of the animal body as being capable of stimulation by all known physical agencies, but the degree to which a part of the body, or integument, may be irritable to some agencies may be relatively great, while the same part may only be irritable to other agencies in an infinitesimal degree.

In general there is a "threshold" of stimulation. This means that when the stimulus falls below a certain intensity, or is "sub-liminal," the part of the body exposed does not display an observable response. But some parts of the skin, or irritable surface, are differentiated so that they respond to very feeble stimuli of some particular physical kind, while they do not exhibit observable response to other physical agencies even when the latter are relatively very intense. Thus the threshold is lowered, in respect of some specific physical agency, in these differentiated parts and it is raised for all, or most other physical agencies. For instance, the retina in the human eye is very sensitive to light but is shielded from most other stimuli; the skin of the cheeks is very sensitive to heat, but the skin over other parts of the body may be relatively insensitive; the skin of the face may be "burned" by chloroform but not so that of the bare hands, and so on. Thus general irritability rises to "peak value" in the regions of differentiation. Such differentiated regions are receptor organs, or "organs of sensation."

39*a*. THE CLASSES OF RECEPTORS. Receptors are therefore parts, or organs, that are differentiated, or have structure and special properties in the above sense. They occur everywhere in the animal body, but predominantly in the skin. They may

be simple, or provided with accessory parts. They may receive stimuli originating in the substance of the bodily parts, or in the cavities of the body, or from things outside the body but in contact with the latter, or from things situated at very great distances from the body. We thus make classes of receptors.

i. The Distance-Receptors. These are the *visual organs*, or "eyes," which are affected by radiation of a certain, very limited range of frequency, originating perhaps in the most remote parts of the universe; the *auditory organs* which are affected by the vibrations of material bodies, such as sound-waves in the atmosphere or in water: such vibrations have much lower frequency than has light-radiation; *temperature-organs* in the skin which are affected by radiation of lower frequency than that of light-waves. The distance-receptors place the organism "in touch" with physical events that occur far away.

ii. The Near-Receptors. Such are touch, or *tactile organs* in the skin and elsewhere—these are affected by contact with material things; *Taste-organs* in the tongue and palate, *chemical receptors* in the skin of lower animals, *olfactory organs* in the mucous membranes of nasal cavities—these three kinds of receptors are affected by some chemical (soluble) substances that come into actual contact with them and set up chemical reactions in addition to mere contact; *temperature organs* in the skin and elsewhere which are affected by actual contact with hot or cold material objects.

iii. Intero-Receptors. The walls of the cavities of the animal body (of course we refer particularly to the body of the mammal) are irritable, that is, they contain receptors. These internal cavities are the alimentary canal (but we have already considered the mouth and pharynx); the pericardial and pleural cavities; perhaps the cavities of the heart and blood-vessels; the bladder, ureters, urethra and vagina. General sensation, and pain, may be the results of stimulation of these receptors.

iv. The proprio-ceptors. In most of the cases already considered the receptors are stimulated by things and agencies that are really outside the bodily tissues, but in the cases of the proprio-ceptors this is not so. There are receptors in the muscles and joints which are stimulated by variations of tension (of a muscle),

or by pressure (on the surfaces of a joint), or by chemical changes in the tissues themselves. The membranous labyrinth in the internal ear of a vertebrate animal has receptors that are stimulated by changes in bodily posture. In most invertebrate animals there are receptors contained in organs called otocysts, or statocysts, and these are also stimulated by changes of posture. Thus the agencies that affect the proprio-ceptors are those of the animal body itself and not of the outer environment.

39*b*. THE NATURE OF A RECEPTOR ORGAN. Essentially, and in its most simple form, a receptor consists of one or more nerve-terminations (see Sections 12, *f*, *g*). But, as a rule, the organ has *accessory parts*. Thus the essential visual receptors in a vertebrate are the rods and cones in the retina : each of these is connected with a chain of neurones (see Section 40*a*) which is the peripheral part of the optic nerve tract. But they are disposed, in the eye, as one surface of a membrane or retina, and the ball of the eye, with lens, pupil, iris, etc., constitute the accessory visual apparatus and are instrumental in causing an image to fall on the retina in the same way as the photographer's camera causes an image to fall on the sensitive plate. In a statocyst, as we find it in, say, many molluscs there is a sac which contains a little rounded stone. There are receptors, or nerve-terminations, on the internal wall of the sac. Changes in the posture of the animal cause the little stone, or otolith, to press now upon one side of the sac and again on some other side, and so on.

Artificial accessory parts. Such apparatus as spectacles, telescopes, microscopes, telephones, ear trumpets, spectroscopes, cameras, microphones, wireless receivers, thermometers, etc., are contrivances that extend the range, sensitivity, etc., of the natural accessories of receptor organs. Thus normally a very small quantity of light enters the human eye and so the stimulation of the retina may fall below the threshold when a distant star is looked at. But a telescope is a contrivance that interposes a large lens between the distant object and the eye, so that a much greater quantity of light is made to fall on the retina. Thus a subliminal stimulus can be magnified in intensity so as to affect the receptors in the retina.

In the case of a wireless receiver electro-magnetic waves of very high frequency are concerned. We have no receptors that

are affected by these waves, but they can be made to transform so that the final result is sound waves of audible frequency.

39*c*. The Physical Nature of Stimuli. Those agencies in nature that affect the receptor organs are gravitation ; contact with material things ; chemical substances (salt, sugar, quinine, etc.) ; electric currents and charges ; perhaps magnetic fields ; radiation of a certain frequency (for light) ; radiation of much higher frequency (X-rays) ; radiation of low frequency (heat) ; actual contact with cold or hot material bodies and so on.

Thus we can speak of gravity-receptors, tactile-receptors, sound-receptors, chemical receptors (in the taste and smell organs), pressure-receptors, electric receptors and so on.

39*d*. " Reception " in General. It has become customary to speak of a sense-organ " receiving " stimuli, but what happens is that the nerve-terminations in a receptor organ simply react with some other agency. Thus when salt is placed on the tongue there is a chemical reaction between the sodium chloride and the materials in the nerve-termination ; when light falls on the retina the radiation does much the same thing as light does when it impinges on a photographer's sensitive plate, that is, some definite chemical reactions occur ; when a prawn stands on its head gravity causes the otoliths, or liquids to impinge on different nerve-terminations than when the animal is the right way up. And so on, the stimulation of a receptor organ is not merely something " received " or " impressed " by or on the animal (as when water is poured into a vessel, or when a stamp makes a device on plastic wax). The materials of the receptor participate in a positive reaction with something in the environment.

Essentially a vertebrate visual receptor does not differ from a photographer's camera ; an auditory organ is physically the same kind of thing as a microphone and a taste-bud on the tongue is comparable with a slip of litmus paper. The animal body simply reacts with the things in its neighbourhood in essentially the same ways that any other physical thing does. But, because of the extraordinary physical complexity of the system called an animal body, the variety of the reactions, and their delicacy as regards the quantities of energy involved, transcend most inanimate reactions. Thus the smell of, say, chlorine can be experienced when the concentration of the gas

in the air inhaled is far too small to admit of a purely chemical test. Perhaps the detection of electro-magnetic radiation by the grid of a thermionic valve that is included in a wireless receiver involves smaller quantities of energy than in most physical tests, yet it is probable that the analogous organic process—the affection of a synapse by a nervous impulse (see Section 41*a*) is far more delicate.

The " reception," in the strict sense, involves the nerve-terminations in the sense-organ, and there are many examples of bare and simple reception in this sense. But in the higher animal these conditions are superadded to such simple reception.

i. The accessory parts of the sense-organs amplify, block, analyse, or otherwise modify the energies that fall upon them. Thus taste-buds on the tongue amplify the chemical changes that are the basis of the sensation of taste : we do not taste many things on the lips. These receptors also analyse, so that there are many different kinds and degrees of taste. So also with smell. The accessory parts of the eye act so as to set up an image on the retina such that there are parts in this image which have " one-to-one " correspondences with the parts of the environment that are in the field of view of the eyes. The organ of Corti in the internal ear analyses the total body of sound that is conveyed into the perilymph surrounding it so that a multitude of vibrations of different frequencies are received separately by the nerve-terminations. And so, on the other hand, small changes of temperature do not affect the retina, nor the pain spots in the skin, nor the pressure receptors in the joints, etc. The multitudinous agencies acting on the animal body are therefore partially isolated from each other, minimized or magnified and are received, to some extent, apart from each other.

ii. The receptors are localized in the animal body. In many animals all the external parts may be equally irritable, or generally receptive—this is probably so in the case of an Amœba, for instance. But in the amœba, and to a less extent in many other animals there is no very pronounced orientation of the bodily parts. In the vertebrate animals, however, the body typically moves so that the cranial extremity precedes and so there are right and left sides. It moves on limbs so that there are upper and lower surfaces. There is paired symmetry in most organs (right and left limbs, lungs, kidneys, etc.). Therefore the

specialized sense-organs (eyes, auditory organs, taste and smell organs) tend to be situated in that part, or head, which precedes the other parts in motion. And, since in moving forward by paired locomotory organs, the animal experiences fields of force to right and left, there is a corresponding bi-lateral symmetry in the great distance-receptors.

39*e*. THE CONDUCTION OF STIMULI. The receptor organ is essentially the termination of a nerve-fibre (Section 12*g*). This termination, of many different forms, or structures, is different from the rest of the nerve-fibre. It is the termination that is stimulated by, or reacts with the external physical agency. But being affected by, or changed by interaction with the external agency the nerve-termination originates a physical disturbance called the *nervous-impulse* and this is propagated along the remainder of the nerve-fibre.

Thus when a sense-organ is stimulated an impulse is set up in the nerve " attached to " it and this impulse travels up into the central ganglion in which the nerve ends. Everywhere in the body of the higher animal, but mainly in the head and in the skin in general, there are receptor organs that are susceptible of being stimulated by physical events occurring in the cavities of the body, in the bodily tissues, on the surface of the skin, outside the body and at the remotest parts of the universe. In the higher animal, and particularly in man, it is these latter distance-receptors that have become of increasing significance. In civilized man those natural and artificial receptors that are stimulated by radiant energy have now become the chief means whereby he comes to act upon and know his environment, while the near-receptors have become of less significance. Smell and taste now count far less than hearing, and hearing is of less significance than is the reception of electro-magnetic radiation.

Whatever they may be, the stimuli that originate in the receptor organs are conducted to the central ganglia *via* the afferent nerves.

40. *ON NERVOUS CONDUCTION*

Events occurring inside or outside the animal body stimulate receptor organs, which are essentially the peripheral ends of afferent nerves.

40*a*. The Anatomical Conception of the Neurone. Whatever it may be, a nervous structure is made up of units called neurones.

A neurone consists of a nerve-cell which has at least two poles. From each pole proceeds a fibre, or axon. Each of these fibres breaks up into arborizations, or branches, or dendrites. One of the fibres may be long. In 1 a typical neurone is represented as beginning in a bunch of dendrites, such as a receptor organ in a muscle, and as being prolonged into the nerve-fibre, or axon, which then passes into a nerve-cell. From the latter issues another fibre of variable length and this breaks up into another series of dendrites. In 2 there is shown a

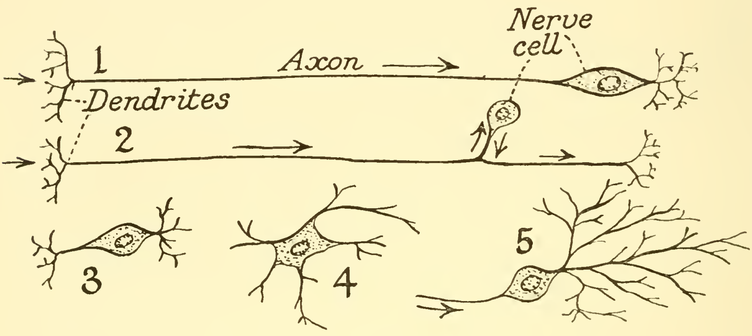


Fig. 19.

1, A typical neurone; 2, a neurone with a unipolar cell; 3, 4, 5, neurones in ganglionic centres.

similar structure. The beginning is a series of dendrites, which may be a touch-receptor in the skin. This is prolonged into an axon which is one fibre in a nerve running from, say, the tip of the finger up to the brachial plexus in the armpit and then into the spinal cord. Just before the fibre enters the cord it passes into and then emerges from a bipolar cell and the fibre leaving the cell breaks up finally, in the spinal cord, into a series of dendrites.

In 3 and 4 are represented neurones which consist predominantly of nerve-cells. These cells may be bipolar (as at 3), each pole consisting of a bunch of dendrites, or it may be multipolar (as at 4). In these latter neurones the axon may be short, or hardly distinguishable.

All neurones are polarized—that is, the nervous impulse that traverses them goes in one direction only, as indicated by the arrows in the figures. At 2, for instance, some physical agency affects a receptor, or nerve-termination, or bunch of dendrites, as shown by the short arrow. The physical disturbance in the receptor then initiates another physical disturbance, or nervous impulse, in the axon and this travels along the latter with a velocity of about 40 to 100 metres per second until it reaches the nerve-cell. Passing through the latter it breaks up in another bunch of dendrites somewhere in the grey matter of the ganglion, or part of the spinal cord. No observation suggests that the direction of a nervous impulse in an axon is ever reversed.

Now, whatever they may be, all units in the nervous system, peripheral or central, are made up of neurones and a neurone is always a nerve-cell with its dendrites. One set of dendrites is afferent, that is, impulses pass through them into the cell. The other set of dendrites is efferent, that is, impulses pass into them out of the cell. A nervous path in the nervous system consists a ways of several or very many neurones placed end to end.

40*b*. THE NERVOUS IMPULSE. We do not know what precisely is a nervous impulse. It is certainly a physical disturbance established by the stimulation of a receptor organ and then communicated to the materials of an axon. A nervous impulse is accompanied by an electric disturbance, in this way,—let $\underset{\rightarrow}{a}\ \underset{+}{a}\ \underset{-}{a'}\ \underset{+}{a}\ a\ \underset{\rightarrow}{a}$ be a small part of an axon and let the arrows indicate that an impulse travels along the axon, or fibre, from left to right. As the impulse passes each small segment, say a', of the axon, that segment becomes electrically negative with respect to the adjacent parts of the axon, which are positive. The impulse may be compared with the current passing along an electric conductor, with the flash that passes along a train of gunpowder which is fired, with the jolt which passes along a train of wagons when the engine suddenly starts, with the wave of vibration transmitted along a rope when one end of the latter is twitched, etc., but it is none of these things. From our present point of view a nervous impulse conveys a stimulus that originates somewhere by a change in a receptor organ.

Whatever it is, there is no doubt that it is a physical process (that is, it is not a thought, or idea, or psychosis). In general, then, the physical disturbance that is initiated by some agency that reacts with a receptor organ travels along a chain of neurones, that is, a nervous conductor, or nervous tract, or simply a nerve, until it reaches a " nerve-centre."

41. *ON GANGLIONIC CENTRES*

There need not be any anatomical structure called a " centre." In many lower animals, such as the medusæ, or even in the walls of the alimentary canal of the higher animals, the nervous system consists of a continuous nervous network and the receptors are connected with this by short nervous paths, while the effector organs are similarly attached. Of such a nature is the primitive animal nervous system or " nerve-net." But in all the higher animals there is also a system which is differentiated into peripheral and central parts: this is the synaptic nervous system. There are two halves of the peripheral system, (1) *the afferent nerves*, which begin in the receptors and lead *into* the *central ganglia* and (2) *the efferent nerves*, which begin in the central ganglia and lead *out from* the latter to the effector organs.

41*a*. The Anatomical Conception of the Synapse. If we trace the axon from a single receptor we find that it terminates centrally in the spinal cord, or brain, or in other nervous centre, or ganglion (Fig. 20, 1). The termination is in a synapse.

At the synapse two bunches of dendrites come into relation with each other so that the branches of the arborizations interdigitate with each other but do not actually touch each other. That is, between the ingoing, or afferent neurone and the outgoing, or efferent neurone there is tissue, or material which is non-nervous and the impulse, in passing through the ganglion jumps, so to speak, from one set of dendrites to another.

This is the very simplest conception of a synapse and it is probably only a convenient fiction. What we actually have is indicated in Fig. 20, No. 4. That is, a nerve-fibre entering a centre has synaptic connections with several, or many other fibres entering or leaving the centre.

41*b*. Ganglionic Centres. Thus receptors are the terminations of nerve-fibres: Fig. 20, 2 and 3.

Both figures represent actual conditions: a receptor may be the dendrites of one neurone (as in touch-receptors) or it may be a chain of neurones (as in the retina of the eye). But in actuality the dendrons or conducting fibres of many receptors are all bound up together to form a nerve. The nerve after following a more or less prolonged path in the body enters into the spinal cord, or brain, and then each of its fibres, or each of the branches of a fibre, ends in a synapse. All these synapses in which one, or several, nerves end constitute a ganglion. And

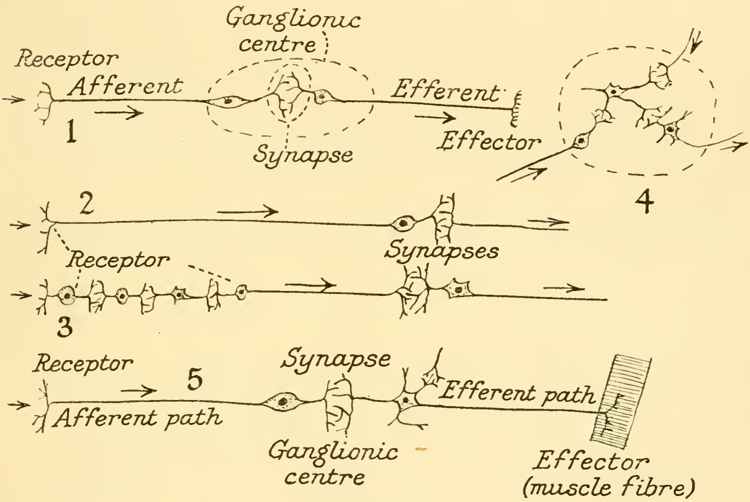


FIG. 20.

1, Diagram of the simplest conceivable neuro-muscular mechanism; 2, connections of a receptor; 3, the same, but the receptor is a chain of neurones; 4, connections of neurones in a ganglionic centre; 5, the simplest conceivable reflex arc.

as Fig. 21 shows, there are always other nerves, or nervous, or conducting tracts entering into the same ganglion. A ganglionic centre is therefore the junction, *via* a multitude of synapses, of two, or many nerves.

And all receptors are thus the terminations of afferent, or ingoing, nerves that end in ganglia which are the predominant structures in the spinal cord and brain of the vertebrate animals or simply the cerebral, or segmental, or other ganglia of the invertebrates. These structures we shall consider more fully later on.

42. *ON THE EFFECTOR ORGANS*

The parts of the animal body that are visibly and immediately active in behaviour are limbs, jaws, teeth, etc.—all those instruments that we have considered in Sections 23–4. Subservient to them, in the sense of supplying energy, are the organs of assimilation, respiration, circulation, etc.—these also we have considered (Sections 12, *b-c*). The elementary agencies of behaviour are not apparent on mere inspection of the active and living animal—they are the muscles that actuate limbs, wings, jaws, etc.; that cause the heart to contract and relax; that regulate the calibres of the blood-vessels; that actuate the respiratory organs, etc. Along with them are the glands—those that secrete saliva and other digestive fluids; that elaborate the internal secretions; that are concerned in general metabolism; that make poisons, etc. The muscles and glands are the effector organs.

Effectors do not function by themselves but must be stimulated to activity by nerves—they are *innervated.* Thus there is another side to the sensori-motor system: stimuli originating in the receptor organs set up nervous impulses which enter the ganglia *via* the *afferent* nerves. In the ganglia these impulses traverse synapses and then set up other impulses in the *efferent nerves.* These then stimulate the effector organs to activity. Thus the whole process of an element of behaviour involves

→ Receptors → Afferent nerves → Synapses in the ganglia → Efferent nerves → Effectors.

42*a*. The Anatomical Conception of the Reflex Arc. A reflex action may be illustrated by the experience of "blinking." Something is thrown against a man's face when he immediately closes his eyes momentarily. The stimulus is the moving object, the receptors are the eyes, the afferent nerves are the optic ones, the ganglia are in the brain, the afferent nerves are those that go to the muscles of the eyelids, which are the effectors.

The "simple" reflex arc is an anatomical fiction cherished because of its value in exposition: it represents the simplest conceivable mechanism capable of carrying out an elementary act of behaviour. Fig. 20, 5, shows that at least two neurones

are necessary: (1) that which has a receptor as its peripheral termination and (2) that which has a "motor-plate" (in a muscle) as its peripheral termination. Some physical agency reacts with the receptor and initiates an impulse which flows along the dendron, or afferent path, into a synapse in the ganglion. There the impulse passes through the dendrites into the motor-cell and then along the axon of the latter, or efferent path into the motor plate which is its termination in the muscle-fibre. The change thus set up in the motor-plate stimulates the muscle-fibre to contract, that is, somehow it releases potential energy in the latter effector organ.

The description is a fiction (1) because more than one receptor is involved in the original stimulation, (2) instead of one dendron there is really a number of such making up a nervelet, (3) there are many synapses, many efferent axons and many muscle-fibres. But even then the scheme is much too simple.

The actual reflex arcs. We may approximate further towards actuality as follows:

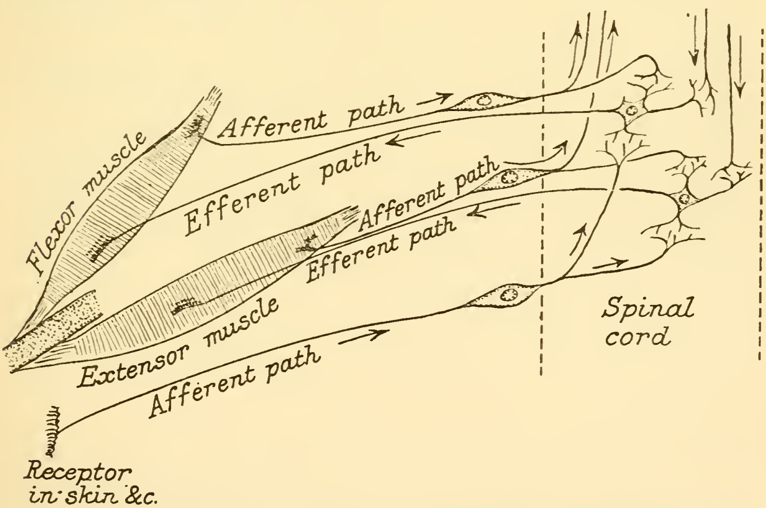


FIG. 21.—DIAGRAM OF THE MINIMAL COMBINATIONS OF NEURONES IN AN ACTUAL REFLEX ARC.

The reflex may be the kicking movements of the hind leg in a sleeping dog when the skin of the flank is tickled. Two sets of muscles are the effectors, (1) those that flex the leg and (2)

those that extend it: in all cases when a muscle contracts an antagonistic muscle relaxes, and *vice versa*, thus two efferent, motor tracts are involved and two sets of synapses in the ganglion part of the spinal cord in this case. Only one receptor (in the skin) is shown, but there are very many, for the reflex act may be elicited by tickling a considerable region of skin. But the reflex (in general) may also be elicited from other parts of the body and so another afferent path is also indicated. Further, many analogous reflexes may be obtained by stimulating the side of the body opposite to that on which the effectors are placed and such paths are not shown. When a muscle contracts its proprio-ceptors are stimulated and so afferent impulses from the contracting muscle itself are sent into the ganglion—these are also indicated in the diagram. Lastly, the reflex may not occur if the dog notices that he is being teased (or he may do something else—growl or bite) and so there must be efferent paths from the brain (the higher ganglion) to the region of spinal cord concerned (the lower ganglion) and impulses descending these latter paths may arrest, or inhibit an incipient, or potential reflex act: these latter paths are indicated.

Thus any reflex scheme must be simplified to an extraordinary degree before it can be represented diagrammatically.

All elements of behaviouristic activity are effected in some such way (remembering the limitations of description suggested above). Chains and combinations of reflex acts make up complex bodily activities. In a limited way such mechanisms as are indicated here may *completely* describe behaviour. In all cases they are the *means of behaviour*, though what we shall call "experience" profoundly modifies the workings of these nerve-muscle mechanisms. Presently we shall return to this subject of reflex activity.

II. SENSATION AND PERCEPTION

When a receptor organ is stimulated a change in the state of consciousness of the animal may be experienced: if, for instance, there is a lightning flash, followed by violent vibrations of the atmosphere, we may "have" the sensations, or sense-impressions, or changes of consciousness which we call light and sound. In this case the "having" implies both sensation and perception.

But in much of our experience as living organisms the stimulation of receptor organs is not followed by any such changes of consciousness. Thus when one is in a state of deep sleep a multitude of receptors are still being stimulated (atmospheric vibrations, for instance, still affect the auditory organs), but there is no consciousness. In ordinary, aimless waking activity there is no doubt that a vast amount of receptor stimulation is not consciously experienced. And in the performance of some learned, automatically effected, muscular task there may be no consciousness of the great variety of stimulations of the visual and tactile receptors, quite apart from the still more complex and numerous stimulations of the proprio-ceptors in the muscles and joints.

43. *ON SENSATION AS A POSSIBLE PHYSICAL PROCESS*

Thus we have to consider what is meant by the sensation that may attend the stimulation of a receptor. We discover that sensation by introspection and, strictly speaking, it is only allowable to me so to discover, or idealize it. But it is really a pretence to take such a (" solipsistic ") attitude on the part of anyone who speaks or writes about it, since he expects that other men and women will listen to him or read what he writes. Living in community with other human persons we must believe that they also have sensations similar or analogous with those that we discover by introspection. And living also in community with some animals, such as dogs, cats and horses, we must also extend to them the same having of sensations. In spite of all that we read in books of philosophy the denial of this conclusion must be regarded as intellectually dishonest.

43*a*. THE TRAIN OF EVENTS IN A CONSCIOUS PROCESS. An organic process, in general, is thought about, first, not otherwise than an inanimate one and we always try to symbolize it by a mathematical equation. For instance, the distance, D, run by a motor-bicycle on a gallon of petrol is a function of several variables ; a, b, c, etc., that is, $D = f\,(a, b, c, \text{etc.})$ where a, b, c, etc., are the calorific value of the fuel, the gradients of the roads, the surfaces of the roads, etc. So also the work (W), done by a man, in riding a push-bike, is a function of the foodstuffs (proteins, fats and carbohydrates eaten), that is, $W = f\,(p, f, c)$.

In the last equation the value of the dependent variable, W, is measured as work done, equivalent to the lifting of a mass, M, through so many feet, L, or the dimensions of W are M and L^2/t^2. So also the calorific values of the food eaten can be expressed in heat (calories) which is again equivalent to a mass that is lifted through a certain distance against gravity and the dimensions of p, f, etc., are also M and L^2/t^2. Thus the terms on both sides of the equations are of the same denominations.

In physiological investigations we endeavour to represent all organic processes by such equations, and although this is not always practicable it is often possible and we must believe that, given complete knowledge of all the conditions of the process studied, it will always be possible and practicable.

Let something that happens in the outer world stimulate a receptor: there is no doubt that a simple physical reaction between the materials and energies of the things outside and those of the receptor occurs. So also the change that occurs in the receptor stimulates the afferent nerve, the change, or impulse, propagated in the nerve stimulates the synapse, the changes in the synapse stimulate the efferent nerve and the impulse descending the latter stimulates the effector organ, releasing the energy that is potential in the latter, whereupon work is done. All these steps in a behaviouristic process are conceivably representable by equations of the form, $U = f(p, q, r)$, where the terms on both sides are of the same kind, that is, can be made to involve only measurements of mass, length and time, and such equations may apply to some very simple and limited types of animal behaviour.

But when the stimulation of a receptor is followed by a sensation it is not possible to make any physico-mathematical relation between the terms involved, for that term U cannot be made to represent the sensation. It is a state of consciousness which has quality, intensity and duration, but it cannot be symbolized by length, mass and time. It is true that there is a relation of *dependence* between the sensation and the physical events that are associated with it—unless these physical events occur we do not have the sensation. But there is not mathematical functionality in the sense that the dependent variable ($U =$ the sensation) is of the same denominations as are the independent variables ($p, q, r =$ physical vibrations, say) and that for every numerical

change in the latter, the former assumes definite values given by the function, *f*. We may say, therefore, that we only have sensations when the "reasons" for them, that is, certain physical events, occur. But we may not say that the symbolism that describes all inorganic happenings also describes the relation between a sensation and its physical antecedents—that this relation is not that one characteristic of inorganic happening is shown when we know that physical events may, or may not, be followed by sensation.

Therefore we have sensations when, in certain circumstances, physical agencies react with our organs of reception, but the relation between these terms involves the "mind-body" problem and is quite unknown to us in spite of all that has been written upon it.

43*b*. PURE SENSATION is not experienced by us. In our ordinary traffic with the world we have at the same moment many sensations and we cannot avoid thinking about them. Probably we approximate to pure sensation at times. Probably a dog lying on a mat in front of the fire feels warm—supported—comfortable, etc.—all at once. But a man sitting in an easy chair in the same conditions cannot, as a rule, avoid reflecting upon his sensations—and in these reflections he has new states of consciousness which come from his thinking. Sensation, then, is always elaborated into perceptions.

43*c*. CLASSIFIABLE SENSATIONS. When we think about, and make experiments with sensations and their concomitants, and when we study artificial receptors we can make a rough classification of sensations.

i. Associated with the distance-receptors.

VISION. Visual organs. Mere light and shade and darkness in lower animals. Seeing form and colour in man. Probably seeing form but not colour in many higher animals.

HEARING. The auditory organs. Sound with intensity and pitch in man and higher vertebrates. But not always pitch in the lower animals.

HEAT. Temperature organs in the skin affected by radiation.

ii. Associated with the near-receptors.

SMELL. Olfactory organs. Decadent in man and

perhaps blending into general sensation in the lower invertebrates.

TASTE. Gustatory organs. Very similar to smell.

TOUCH. The tactile organs in the skin.

HEAT and COLD. Receptor organs in the skin.

SEXUAL FEELING. Receptors in the external genital organs.

iii. Associated with the intero-ceptors.

HUNGER, THIRST, NAUSEA, DISTENSION. Receptors in the walls of the alimentary canal.

HEART-PANIC. Receptors in heart, pericardial cavity and possibly arteries.

VISCERAL PAIN. Receptors in the muscles of the alimentary canal.

iv. Associated with the proprio-ceptors.

MUSCULAR SENSE, PRESSURE, WEIGHT, EFFORT. Receptors in the muscles and joints.

RHEUMATIC PAIN. The same.

VERTIGO, BALANCE, DIRECTIONAL SENSE. Receptors in the internal ear.

The classification is necessarily an obscure one and we are hopelessly shut off from ever knowing, with any probability, the sensations of animals other than man. And even the nature of some sensations may be communicable between man and man only imperfectly—as in the notion of normal colour sensation that may be acquired by a colour-blind man. The list must be regarded as merely indicative of the kinds, or qualities, of sensation had by normal human animals.

And it is seldom, or never, that we have such a single quality of sensation unmingled with others. We come by the rude classification by acts of attention. We exercise mental analysis, assisted by experimental devices and then we " proceed to the limit " and arbitrarily isolate from their sensational context each pure, or indefinable quality. No one such sensational quality can be described in terms of any other—seeing has nothing to do with hearing, redness with blueness, heat with cold and so on. " Colour-tone," etc., are only terms used to express rough analogies.

43*d*. NERVOUS ENERGIES. It is, of course, an insoluble problem why the nervous impulse proceeding from, say, a visual receptor may be accompanied by the sensations of light and colour

while that coming from an auditory receptor may give us sensation of sound. So far as we know, every nervous impulse, in any nerve whatever, " sensory " or " motor," is the same kind of molecular disturbance of the materials of the axis-cylinders, and is always accompanied by dissipation of energy, just as in the cases of other molecular processes of the same general category —that is, some production of CO_2, however small, seems to be a condition of the propagation of nervous impulses.

It is, perhaps, significant that a nervous current passing along a nerve should be constituted by unitary impulses succeeding each other with a certain frequency. It may be significant that this frequency of nervous impulses appears to be different in different nerves. We are reminded that the physical events that stimulate receptors may also differ in frequency, thus low-frequency radiation is felt as heat, higher-frequency radiation as red to violet light, the colour varying with the frequency. And even the material impulses that stimulate the auditory receptors have varying frequencies and the pitch of the sound sensations that follow these impulses depend on the frequencies of the atmospheric vibrations.

But again we have no notion at all why the qualities of the sensations of light of various colour should depend on frequency of nervous impulse, *if* that should indeed turn out to be the case.

43*e*. THE MECHANISM OF RECEPTION IS NOT SEPARABLE FROM THE MECHANISM OF BEHAVIOUR. There is no such thing as a receptor mechanism *by itself*. A receptor and its afferent nerve always stand in structural connection with a series of synapses that are in structural connection with a series of efferent nerves and their endings in effector organs. That means that reception itself does not exist in the animal organism but is always part of the apparatus of action. And it may be doubted whether we ever have sensation resulting from the stimulations of receptors unless these stimuli, translated into nervous impulses, impinge upon the nerve-centres and are followed by action of some kind. That action may be only virtual—the stimulation of the nerve-centres " sets the points," so to speak, in order that something may happen in the effector organs. It appears, from all that we know of cerebral physiology, that the sensory system was evolved for the " purposes " of behaviour and not merely for

passive contemplation of the events that occur in the environment. And we know, of course, that purposeful behaviour, involving the whole sensori-motor system, may proceed without sensation passing into consciousness.

43*f*. THE UNITIES OF SENSATION. Since there are very many kinds of receptors functioning at the same time it follows that we generally have a multiplicity of sensations all more or less passing into consciousness. Such complexes are integrated into unities and these are what the animal reacts to in its behaviour. A complex of sensations acquires significance and is individualized as the antecedent to bodily action of some kind. Thus in crossing a street in busy traffic the visual and auditory organs must transmit innumerable impulses to the nerve-centres, but only a few of these can receive, or indeed demand, attention and response in action. The visual impressions of several vehicles; their proximities, directions of movement and velocities; the sounds of motor horns; the movements of the policeman on point duty—these sense-impressions are integrated as sensational unity which is then attended to while experience suggests the appropriate bodily response.

43*g*. THE INTUITION OF DURATION. What we call duration (or "time") is the consciousness we have of the passage of nature (see again, Section 2). A purely physical system of things passes in that its available energy (and thus its inherent physical causality) becomes less and less as the system tends towards stability. But the organism *resists* the passage to physical stability and it remains a permanent centre of causality—since it is not only an individual thing but a succession of living things constituting a race. The consciousness of this resistance to physical degradation is our intuition of duration. It is cumulative in that the phases of the passage of nature persist as memories, as motor habits and as instincts. It is cumulative in that the present phase is not merely the superposition of the past phases but is an integration, and always something new, and it is in this sense that Bergson speaks of duration as creative. Nothing can be more immediate, or intuitive, than the duration of the animal since, being the consciousness of that which distinguishes the animate system of things from the inanimate one, it is life itself.

"Time" punctuates duration by referring the organic phases

to events that occur in the external world that is (more or less) " made." The intervals of duration called days in the life of a man are not, in general, the same to him since " time passes " more or less quickly, and the part of the passage of made inorganic nature included between two successive transits of a fixed star is taken as the standard interval of duration. Days, minutes, seconds, years, centuries are points in the passage and duration lies between these points. Much occurs in the life of a child between two midsummer-night star transits and so " time is long " ; less occurs, in the same astronomical interval, in the life of an old man and so " time flies." Astronomical time, then, is the framework in which the things that happen to the animal are inserted.

43*h*. THE INTUITION OF SPACE. Space is the consciousness of bodily mobility. All the movable things in the body of an animal have receptor organs in them and so we have sensations of the movements of these parts. Primitively, no doubt, the sensations of the tensions of muscles that act against resistances are parts of the mechanisms of behaviour. Thus when a man uses a screwdriver he feels the resistance of the materials as he forces the screw into its bed and he graduates the muscular tension to avoid " stripping the thread." It is possible that in behaviour on a low plane all this delicacy of action is automatic and does not rise into consciousness. But in the higher levels of behaviour the consciousness of the movements of the body becomes intuition of space.

The perception of space apparently comes from many species of receptivity. There is spatial consciousness apart from vision and had merely by walking, when the movements of the limbs give us the intuition that the body which was formerly *there* is now *here*, and the magnitude of the interval between " there " and " here " is felt from the amount of muscular force exerted, while there is a parallel intuition of duration between the " then —there," and the " now—here." Similarly the space-interval is felt when the hand moves along, say, the paper on which one writes, even when there may be no vision. Here again the consciousness of muscular movement is had. There is intuition of space had by hearing when one can make rough estimates of the " place " from which the sound comes by movements of the

head (when, however, muscular movement is again the origin of the intuition). Doubtless there is space-intuition from the actual or virtual movements that occur during the reception of stimuli by the internal ear (the " labyrinth ") and the consequent stimulation of the cerebellum, which controls the " tonus " or normal tension of the skeletal muscles. There is obscure space-intuition (" direction ") when a man, lying prone on a turntable that can be rotated with negligible friction, and with exclusion of visual and auditory stimuli, can roughly estimate the angle through which his body is turned. Here there is consciousness (*via* the muscle and articular receptors) of the inertia of the body.

Mainly space-intuition comes from consciousness of the activities of the eye-ball muscles. [It is extraordinary that these six pairs of muscles, each pair representing a nervous segment, are about the most constant of all morphological characters of the craniate vertebrata.] In all space-intuitions there are minute and most delicate motions of these muscles. The estimate of the length of a line up and down or side to side comes from the movement of the optical axes set up by the eye muscles. The estimate of the area of a circle or other figure comes from the movements of the optical axes round the periphery. Distance in the direction right-ahead comes from the varying inclination given to the two optical axes and probably also from the movements of the muscles of accommodation that are instrumental in focussing the eyes. And so on. Visual space-intuition is to be completely described in terms of the consciousness of the activities of the ocular muscles.

The " field of space " that we intuite directly from natural, unassisted bodily muscular activities is small. A man may only move his body, by walking, through (say) 30 miles in a day. He might walk across a continent and then (conceivably) swim an ocean and so attain intuition of the spatial magnitude of the earth, in a few years. He may only see round about him for a few miles. He may appreciate the angle subtended by a sixpenny-piece if it is only a few yards distant. But the artifacts which man uses enormously increase his visual field so that space comes to be represented in " light-years," when man reaches out into the cosmos. But here again the intuition of these greater spaces

comes from muscular activities: The measurement of the diameter of a fixed star involves the adjustment of scales in the astronomer's apparatus and this is no different in principle than the muscular activities and adjustments in the optical axes of the eyes when we look at more or less distant objects.

And all cosmic spatial estimates are also based on bodily movements. All such estimates make start from a terrestrial "base-line" which is only a distance along which a man can walk in an hour or so. It is true that the distance is measured with extraordinary accuracy—far more so than could be attained merely by "stepping-off" the base-line. The standard of distance is a "made" thing which we take as unchangeable. Just as the standard duration is that, between two successive transits of a fixed star so the standard distance is that of a metal rod ("corrected" for temperature). Two or more of these rods are laid end to end and their "ends" are not placed in contact but are laid near to each other and the distances between them are measured by a microscope. We obtain these latter space-intervals again by the adjustment of scales, that is by bodily muscular activities. The rods are put end to end in a "straight line" between the extremities of the base-line and the straightness is that of the ray of light passing between telescopes at the ends of the base-line. The ends of the rods are adjusted (by screws, scales, etc.) so as to lie in this straight line. All further trigonometrical and celestial space-estimates involve the use of this base-line and the adjustments, by bodily muscular activities of apparatus that are really artificial receptors.

43*i*. THE "FORMS" OF SPACE AND TIME. The mathematical space (of the Newtonian period) was 3-dimensional. There was motion in space from side to side along the axis $-x \longleftarrow o \longrightarrow +x$ (parallel to the lower margin of this page), motion in space, up and down, along the axis $-y \longleftarrow o \longrightarrow +y$ (parallel to the right-hand margin of this page) and motion in space backwards and forwards, along the axis $-z \longleftarrow o \longrightarrow +z$ (perpendicular to the page). Mathematical expressions involving these motions were the same in form irrespective of the $+$ *ve* and $-$ *ve* signs (except when negative quantities might become positive ones by squaring). Thus mathematical space, or extension, was "isotropic," or the same in any direction.

Obviously the actual space of our intuition is non-isotropic. A man always walks (that is ordinarily) ahead in the direction $o \longrightarrow + x$, that is, o is where he starts from and he walks in the direction of the relaxed axes of his eyes. He does not " skid " from side to side as a rule but turns his body so that he still walks ahead. He can only move up and down with difficulty (say by jumping) and then his range of movement is very limited. Right and left are, in actuality, different, partly because of his bodily asymmetry and partly because right-handed and left-handed things (such as gloves, cyclones and anticyclones, etc.) are not the same and cannot be superposed. Thus his space-dimensions are anisotropic.

Duration has only one dimension—past and future. Time, to the mathematician, is the same in the past as in the future, the formal difference being $- t$ and $+ t$. Eclipses can be calculated in past time by the same expressions as in future time. Duration is thus extension and in the mathematics of relativity it is only the fourth extensional dimension (being made so by a mathematical artifice involving the " imaginary," i).

But the fundamental thing in life is duration that is one-directional and irreversible. Time has " an arrow " given by the entropy-law. An animal continually grows old and never grows young again. Mathematical time (says Oliver Lodge) is as a roadway, but duration is as a river. We can turn back along the road, but we can only turn back on the river when we oppose the resistance of the current.

The multi-dimensional geometries and the apparent paradoxes of relativity-theory have become conceivable because we can now imagine, and partly realize velocities of motion that transcend those of the Newtonian period. To the old-fashioned biology, based on Newtonian mechanics, there are still three dimensions of anisotropic space and a single dimension of irreversible time. But it must be most clearly realized by the student that space and time intuitions are not unchangeable *but evolve*. As our domination over nature, and our powers of moving more and more quickly increase, so our intuitions of space and time must change. The complexities of relativity-theory come from the potential increase of such powers indicated by the equations of the newer physics.

44. *ON THE MIND AND ITS OPERATORS*

From the naïvely biological standpoint it is convenient to postulate a mental mechanism or mind. The mechanism is not cerebral in the strict sense—that is, it is not what is implied in receptors, peripheral and central nervous systems and effectors. The mind is not a *tabula rasa* on which experience writes, neither is it something which has ideas before it has experience. It is a mechanism in that it does not operate " anyhow " but in an orderly and typical way. It exhibits type in that it is " the same " in groups of animals that can be arranged into morphological categories. It is " the same " in all the animals of the same categories (say dogs, horses and men) within the limits imposed by fluctuations, mutations and secular evolution. It is evolved and is not invariable in the strict sense and mental operators may be individually developed by trial and error, or they may be " acquired " (see Section 87).

We can best discuss the mind as a bundle of " operators " which we can arbitrarily isolate by introspection and consider, by analogy, in other animals than ourselves. But actually the operators integrate so that the mind is a unity. The operators deal with the raw materials of sensation *after* these have been intuited and inserted in the frameworks of duration and space. The operators we may divide into the elementary ones of quantity, quality, relation and modality—these are the famous Kantian " categories of the understanding " and no scheme seems better to assist in biological investigation. But human evolution has given us secondary, or acquired categories, or operators, and these we shall also consider.

44*a*. The Elementary Operators.

i. Quantity. The mind has in it, with respect to the sensory data received, the consciousnesses of one thing, or many things, or of the degrees of manyness, or number. A pack of cards is *perceived* as one thing, but it is decomposable into many things —a unity of 13 spades, 13 clubs, etc., or 52 different things.

ii. Quality. The things are different in respect of their quantity, 52 cards or 13 spades, 13 clubs, etc. But they are perceived as not alike in quality, a spade being different from another spade just because there is one spade and another spade.

But one spade differs from another one in that one is the ace and another is the king—this is qualitative difference the perception of which is obviously some other mental operation than that which gives the perception of one ace of spades and another ace of spades.

iii. Relation. The things having the same quantity and quality may be arranged differently. Thus 13 spades may be perceived in the relation—ace, king, queen, knave, 10, 9, etc. or they may be perceived as ace, king, 2, queen, 3, knave, 4, 5, 6 . . . 10. And so on.

iv. Modality. Not having a pack of cards we may have the consciousness of obtaining one—that is *possibility*, or we may actually have the consciousness of the *existence* in perception of the pack. But it is not *necessary* that we should have it, though life gives us the conviction that many things are necessary.

(Such are the elementary operators and we do not know of living animals in which they do not enter into the mental mechanism, in some grade of activity. The illustrations are trivial ones, but the student may easily find others from ordinary, essential experience.)

44*b*. THE ACQUIRED OPERATORS. In human activities, and to an unknown degree in the lower animals, other operators have been individually acquired, or evolved.

i. Purpose. The mind operates with motive, intention or purpose. The operation satisfies a life-urge, nutrition, reproduction, self-existence. The simple organism may so be active and unconscious of its activity (though the latter may bring a feeling or state of normality, or pleasure), but in mental life the mind consciously operates with these motives of normality or pleasure.

ii. Causality. Expressed crudely there is the mental result that things or events are related as effect and cause. If something happens, something else that is definite in perception also happens. For every particular antecedent event there is another particular consequent event : Events are related in that one depends on some other one. And so on.

Functionality. In its most precise form the operator of causality appears to us in the physico-mathematical *relation* of functionality. There are two events a and b and b is a function of a, or $b = f(a)$. When a happens b also happens and for so much

quantity of *a* there is just so much, and neither more nor less, quantity of *b*. There is an independent variable *a* and there is another variable *b* the occurrence *and magnitude* of which depends on *a*. Now if we do not know *from experience or investigation* that the relation of functionality holds for two variables we cannot assert it *a priori*. Thus pure carbon burns in oxygen with the generation of heat and for so much carbon that is burned there will be just so much heat generated, and we can predict that this will happen from our experience. But we do not know that some hitherto unknown substance will burn in oxygen nor can we predict, even after establishing the bare fact of the combustion, that there will be a definite quantity of heat resultant from the combustion.

In the relation of physico-mathematical functionality the terms *a* and *b* in the equation $b = f(a)$ are stated in the same denominations or are reducible to the same denominations. Thus a gram of pure carbon when burned in pure oxygen generates just so many calories of heat. Then the quantity of heat in calories, *b*, in the above equation is a definite linear function of the number of grams of carbon, *a*, each gram generating just so much heat. Again the momentum of a projectile, *b*, fired from a gun in standard conditions, is a function of the charge of explosive. When the latter is fired, just so much kinetic energy is developed. Kinetic energy is to be stated in terms of mass and velocity and the momentum of the projectile, when it leaves the muzzle of the gun, is also stated in terms of mass and velocity.

Simple dependence. We know, *from experience*, that a sensation is had by us when some particular receptor, or nerve, or nervous centre, is stimulated. (A noise comes from atmospheric vibrations impinging on the auditory organ, *or* from *tinnitus aurium*, when the auditory centre is otherwise stimulated, or from an overdose of quinine.) The sensation " depends on " one or other of these antecedent events, but the sensation cannot be expressed in terms of the motions of the molecules of the atmosphere or of the motions of the atoms, molecules, etc., of quinine : it has nothing in common with these " causes," though it depends on them.

Statistical dependence. Here there is a cause, or series of causes, but there is no one definite effect. When a pack of cards is shuffled (or thrown into " disorder ") and when the pack is cut

any one of the 52 cards may be exposed. We say that there were a multitude of definite small causes which led to the disorder of the cards—these were the unanalysable motions of the hands in shuffling the cards. If we knew precisely all these small events and if we knew precisely all the elements of the movements of cutting the pack we could predict what card would be exposed. In principle this is the same as saying that if we laid a penny on the table head down we should know that when we turned it up we should expose a head. That is, *the relation between the two events is had from our experience.*

So the effect of shuffling and cutting a pack of cards is not unique but multiple and can be expressed as a series of more or less probable events. Non-mathematical people say that these effects are due to " chance " and can be predicted by the probability-equations of the mathematicians. The latter say that the equations are valid because they are confirmed by experience !

Causality is therefore not an *a priori*, or elementary mental operator, but comes *a posteriori* from experience.

iii. Substance. It is practically convenient to distinguish between a thing and its properties, or attributes. The difficulty is to imagine what remains when we divest a thing of its mass, consistency, colour, odour, form and other properties that are apparent in our perception of the thing. The " thing in itself," that is, the substance underlying the properties, remains, said Kant, though we cannot perceive this " noumenon," or thing-in-itself. Thus the physics of a generation ago regarded the substance of the universe as being the ether of space. All material bodies, all radiations and gravitation were modifications, or motions, of this unknown ether which, as a thing-in-itself, could not be perceived. But the ultra-modern mathematical physicists are able to dispense with the notion of the ether and to regard all things as relations. Thus 2-dimensional flat space is simply the relation $ds^2 - g_{11}\, dx_1^2 + 2g_{12}\, dx_1\, dx_2 + g_{22}\, dx_2^2$ where the g's are " potentials," that is values that, being inserted into a certain, very complex differential equation, cause this to have the value $= O$. Matter is just another system of " potentials." Potentials are given from our knowledge of " intervals." Intervals are observed by reading the scales of clocks and other instruments. Clocks and scales are matter, and matter is just a system of potentials, and so on. Here there is no substance,

or ether—though it will be found, on reading contemporary physics, that the investigator rests uneasily on this bed of relations.

He is apt either to roll over on to the ether of space, *or* on to consciousness as the substance of nature, *or* more satisfactorily, to find in that passage of nature which manifests itself in the increase of entropy the substance of the universe.

The Law of Conservation. Plainly, this is just the operator of substance. There is something underlying all physical phenomena that is conserved. It is not matter, or mass, or even energy in the ordinary sense. But it cannot change in total quantity.

iv. Beauty, goodness, truth, etc. What these mental operators are, biologically, we consider in Section 58.

45. *ON PERCEPTIONS*

We see, then, (1) that the animal has states of consciousness, or sensations, when the receptor organs, or the afferent nerves, or the ganglionic centres are stimulated ; (2) that rarely, or not at all does it have pure sensation ; (3) that even then the sensations are inserted, or intuited into frameworks of space and duration. Having " Frames " of space and time are *a priori* and the animal has them before it acquires experience.

(4) It also has a mental mechanism that is arbitrarily decomposable into operators and it has this before it acquires experience just as it has lungs before it breathes, or an alimentary canal before it eats. The elementary mental operators are *a priori.* It has instincts (see Section 54*d*), before it behaves and these potential agents of behaviour are also *a priori.*

(5) It acquires, or may acquire the secondary mental operators.

(6) And all these operators work upon the states of consciousness that are dependent on stimulation of the sense-organs and that have been intuited in space and duration. The results of the elaboration of the sense-space-duration data are perceptions. It is perceptions that we think about.

III. THE PURPOSES OF BEHAVIOUR

By the behaviour of an animal is meant all its activities that we can observe merely by inspection. Those activities are reactions with the things of the environment just as an inanimate system of

things, say a cyclonic disturbance, reacts with the other things that environ it. The tendency of the inanimate reactions is towards disorganization : thus the cyclone dissipates itself. But the tendency of the activities of an organism, or race of organisms, is towards their maintenance, and even their increase in numbers, and towards ubiquity of distribution. This tendency is what we mean by the purposes of animal behaviour.

46. *ON THE LIFE-URGES*

It is convenient arbitrarily to decompose life-activity into the urges or elementary biological categories. These are assimilation, growth and reproduction, and individual self-preservation : they are manifested in behaviour.

46*a*. ASSIMILATION. By this we mean that the organism selects and absorbs materials from its environment, makes these similar to, and incorporates them with, the materials of its own body. At its clearest, assimilation is exemplified by the way in which the green plant absorbs CO_2, OH_2 and inorganic nitrogen-compounds from the atmosphere and soil and, by making use of the degrading energy of solar radiation, synthesizes these into sugar, starch, cellulose, proteins, oils, etc., all of which materials are then reassembled as the tissues of the living plant. So also with other plant and animal organisms in a host of different ways.

Assimilation provides the animal organism with materials that can be oxidized in the processes of metabolism. It is thus that the energy for bodily, behaviouristic motions is obtained. But assimilation is also necessary for growth of the individual body and for reproduction. When, however, an animal has ceased to grow and is not reproducing it assimilates in order to obtain the energy for its behaviour.

46*b*. GROWTH AND REPRODUCTION. The organism tends continually to increase in magnitude and in power over its environment—this is its growth in the most general sense. *Simple growth* means just increase in bodily magnitude without appreciable change in bodily form, and there are short phases in the life-histories of all organisms when simple growth proceeds.

Developmental tectonics. In its embryogeny (see Sections 70, 72) the organism assimilates and, in a sense, reproduces. The

ovum from which it develops divides by mitosis and the daughter-cells divide again and so on. The cells grow in size after they divide and in preparation for the next division. The embryonic cells are assembled into organ-anlagen and then they undergo tissue-differentiation. This is growth with the acquirement of a specific, bodily structure.

Growth with differentiation. And even when the specific pattern of bodily structure has been attained, and while the organism continues to grow, there is usually differentiation, so that it passes through its life-phases and comes to exhibit structure that appreciably changes.

Reproduction. This is essentially growth with dissociation. There is a limiting magnitude to individual growth and when this is attained the organism dissociates some part of its body. It divides by mitosis (in the case of a Protist) or it buds, or it spawns eggs or emits spermatozoa, etc. These dissociated bodily parts then undergo growth in the above senses.

Reproduction with differentiation. Reproduction may be a strictly repetitional process. The cells of a tissue-culture go on dividing—apparently *ad infinitum* and with retention of a specific form—or some races of animals (the Brachiopod *Lingula*, for instance) reproduce so that the generic bodily form has been retained for hundreds of millions of years. But in general there is a slow change in bodily form as the accompaniment of continued reproduction. This is the transformist process.

46*c*. Self-Preservation is the urge to continued individual existence. It is the strongest life-urge. It is limited by inevitable somatic death, either catastrophic or senile death. It is qualified by reproduction which, in a way, prevents individual bodily death but puts a limit to individual acquirements.

47. *ON THE MANIFESTATIONS OF THE LIFE-URGES IN BEHAVIOUR*

Ways of behaving, that is general kinds of bodily motions, may be associated loosely with the urges.

47*a*. Assimilation and its Manifestations. In many organisms the behaviour in assimilating environmental materials is of the very slightest kind. In plants, root-hairs, tendrils, leaves, the petals of flowers, etc., move tropistically (see Section 51).

In many Protists the body is a cell which simply absorbs materials over all or part of its surface. But, in general, animals nourish themselves and in the course of their nutrition exhibit characteristic forms of behaviour. Thus :

i. Hunting for food organisms as in the exceedingly simple way of an Amœba (using pseudopodia), or by the more elaborate methods of a cuttle-fish (the use of the tentacular apparatus, the suckers and the beak) ; or by the craft of a cat, or fox, or man.

ii. Trapping and snaring, with fabrication of the trap or snare (as in the case of the spider's web).

iii. Browsing as in the cases of terrestrial herbivores, many molluscs and some fishes.

iv. Filtration as in the cases of sponges, sessile molluscs, herrings, whalebone whales, etc. And so on, these are only examples of typical ways in which the animal obtains, *via* its bodily motions, the environmental materials which it assimilates.

47*b*. MANIFESTATIONS OF THE GROWTH-URGE. Growth of the body, or of a part of the body, is a functional metabolic activity not strictly to be associated with ways of behaviour in the technical sense in which we use the term. The essential acts of reproduction are the maturations, divisions and fertilizations of germ-cells. Maturations and mitoses are functional activities and, in themselves, the conjugation of two germ-cells, or even gametes, are also functional in the same sense. In the cases of very many animals reproduction is accompanied by little in the nature of behaviour. Thus a Teleostean fish, as a rule, experiences a ripening of its gonads and when the eggs or spermatozoa have become mature they are simply extruded into the sea where conjugation of the gametes occurs at random. In a sessile Barnacle (which is hermaphrodite) the ova and spermatozoa mature in the body, self-fertilization may occur, embryos develop, hatch from their envelopes and are extruded into the sea. The general behaviour of the parent is, so far as we can see, unaffected by all this.

But in a vast number of animals the growth-urge in reproduction is attended by the most complex behaviouristic activities. We notice typical examples : (1) *Breeding and spawning migrations*. Locomotion is involved. Birds make extensive and specially directed flights. Salmon ascend rivers to spawn. Eels descend rivers and seek the mid-ocean to spawn. Cod, plaice, herrings,

etc., congregate in particular regions of shallow sea bottom to spawn. And so on. (2) *Nesting and sheltering.* Here we may note the nests of salmon, sticklebacks and other fishes; the burrows of many insects; the hives of bees, wasps and ants; the nests of birds; the burrows, warrens and lairs of many mammals; the cocoons of silkworms and hosts of marine invertebrates; the choice of hosts by parasitic animals; the deposition of eggs by the parents in host-animals. And so on. (3) *Courtship.* The highly complex activities of birds and mammals that involve song, gesture, etc., in the finding of mates; behaviour of bees and wasps, etc. (4) *Nurture.* Carrying the young in brood-pouches, etc.; suckling the young; feeding nestling birds, etc.; deposition and attachment of the eggs; the provision of food materials—and a host of other curious activities.

47*c*. MANIFESTATIONS OF THE URGE OF INDIVIDUAL SELF-PRESERVATION. Such are *flight* from danger; *fighting* in self-defence; *concealment* in natural cover, or by "smoke-screens" (the "ink" of the cuttle-fish), or by *imitation*, or by *feigning death* by absolute immobility—and so on: there are a multitude of adaptations all directed to self-defence. *Racial preservation* may be included here since the parental generation "leans over the offspring." Again, a multitude of behaviour-activities are included in the general category of parental defence of the offspring.

47*d*. THE ELEMENTS AND PATTERNS OF BEHAVIOUR. A behaviouristic activity that manifests an urge is, as a rule, a complex train of bodily movements. Thus an animal hunting for food becomes aware of the prey *via* the stimulation of the distance-receptors (smell and vision). Adapted movements of pursuit, etc., are the anticipatory parts of the train of movements, which are finally consummated in the killing and eating of the prey. Thus we decompose such a behaviouristic activity into *elements*: locomotion of the body in running and leaping; movements of the claws, jaws and teeth in killing and finally the laceration and mastication and swallowing of the food. The activities, locomotion, calculated approach of the prey, rending motions of the claws and teeth, etc., are the elements of the activity and these elements have *patterns* which are largely dependent on the structure of the animal considered.

We can only illustrate these statements by summary consideration of some elementary behaviouristic activities :

Locomotion. There are the patterns—*Quadrupedal and bipedal* walking, running, leaping as exhibited in the movements of mammals ; *Hopping* in birds ; *Saltatory motions* of many crustaceans ; *Crawling* in such different ways as the motions of a millipede, or those of an Echinoderm (such as a starfish) ; *Burrowing* in the soil by rabbits, moles, earthworms, etc. ; *Swimming* in such diverse ways as by means of cilia (in protozoa), by the swimmerets in a micro-crustacean, or by the fins of a fish ; *Writhing* as in the locomotion of a snail or limpet (where wave-like contractions of a muscular organ, or " foot " effect the locomotion) ; *Rocket-propulsion* as in the squid ; *Gliding and flying* as in fishes, insects, birds and bats. And so on.

Killing. *Biting* with jaws and teeth ; *Biting* that involves the injection of poison (snakes, etc.) ; *Striking* with claws and other bodily weapons ; *Goring* as in cattle and sword-fishes ; *Crushing* as by pythons, bears and cuttle-fishes ; *Stinging* as in the cases of bees, wasps, etc. And so on.

We may regard behaviour in general as expressed by combinations of the elements : locomotion with its variants ; killing ; feeding, fabrication of nests and shelters ; vocalization ; the specialized motions of the external genital organs in copulation and so on. A certain number of such elementary activities are the equipment of all animals. In the well-differentiated categories of animals the patterns of the elements are different—as we have indicated above. The elements are combined or integrated into the behaviouristic activity *that the particular occasion demands* : thus the activity, whatever it may be, is, as a rule, unique in each higher animal, varying from example to example with the environmental circumstances and the animals' experience.

The patterns of the elements correspond roughly with the structure. Obviously flight is impossible to a dog, stinging to a butterfly and vocalization to most fishes. The evolution of the structure of the body must largely restrict the bodily activities and even render some impossible in particular cases.

47*e*. The Versatility of Behaviour. But while structure imposes such obvious limitations on what an animal may do, it is not always possible to deduce the pattern of behaviour from the structure. In simple cases the " behaviour " of a machine

can be inferred from the structure (though not without an indispensable knowledge). Thus we should infer the working of a clock from a knowledge of mechanics, but we should not be able, on this basis alone, to infer the working of a dynamo from its structure (a knowledge of Faraday's laws of induction would be necessary). When we know the structure, with the above qualifications, we can predict how the machine works even when we have not observed it working. This would be the case even if the machine were automatically to regulate itself, for the regulator is of the same order of structure as the other parts.

But we should not infer, from a knowledge of the anatomy of the human body, that a man may be unable to swim without learning ; or, from knowing the human and chimpanzee sensorimotor system, that the latter animal cannot speak ; or, from knowing all the anatomy of a particular parrot, that it does speak. This is because a mental mechanism is concerned in animal behaviour and this is not knowable merely by inspection.

48. *ON THE PURPOSES OF BEHAVIOUR*

We can easily discover, by introspection, that an urge to do something is in consciousness and has in it some feeling of need or desire : thus the nutrition (or assimilation) urge is felt as hunger. It is not simply " had " in consciousness as something that we know—as knowledge that food should be taken—for there is emotional quality, or some consciousness deepening into pain so long as we do not assimilate. On eating the urge manifests itself in behaviour and there is satisfaction. We may think of the satisfaction of an urge like we think of the neutralization of an acid by an alkali in that stability of the acid and base system is effected in the formation of a salt. But we can also easily discover that the satisfaction of an urge in appropriate behaviour does not merely bring about normality of consciousness—it usually gives pleasure. We experience, or have, therefore, needs and desires and we satisfy these needs and desires by behaviour which may be undeliberately effected—as when an infant suckles, or which may be accompanied by conscious states—as when a man scans the menu card in a restaurant, orders his meal and then eats it with the conventional behaviour.

We extend the results of introspective analysis of our own

entire activities to other men and women, believing that they feel and think as we do, have the same desires, needs and the same satisfactions and pleasures as we have when we see that their behaviour, in the same environing conditions, is similar to ours. It is quite impossible to give scientific demonstration of this assurance that we have that other human beings introspect and feel and think very much as we do. The solipsistic attitude denies that we can assert this of other men and women than ourself. Strictly (on this attitude) I alone think and all else—if there is anything else—is the object of my thought. It is not only pedantic but is intellectually dishonest on the part of anyone *who speaks or writes about it*—thereby plainly assuming that other similar thinking human beings exist. Apart from merely playing intellectually with the matter one must come to this conclusion. Further, the demonstration we seek is easily obtained when we reflect that we live in community with other men and women, that we praise or blame, punish or reward them, and contemplate their behaviour not as we contemplate the working of a machine, but with emotion. And from the biological point of view the demonstration is complete since community satisfies the urges of life as we have them. Without the evolution of gregariousness man would not have attained the power over inanimate nature that he now exerts.

We also extend the results of introspection to animals lower in complexity of structure and behaviour than ourselves. Biologically this is strictly justified. All life, as we shall show from the analysis of reproduction, is one thing, and the decomposition into groups and races is only the most convenient way of its investigation. So far, then, as the structure and behaviour of the lower animals resemble those in ourselves, we impute somewhat similar states of consciousness to them and we believe that they have needs and desires and feelings of pleasure and pain. As the structure and behaviour differ more and more from those that we observe in ourselves, so the extension becomes the more difficult.

48*a*. The Organism as a Monad. But even when we reject the solipsistic attitude it is still proper to argue that the organism is a monad. We use the Leibnitzian conception here, not at all metaphysically but in the naïve biological sense.

(1) The universe of an organism is simply all those things with which it has relations. Thus the universe of a Bacillus may be

little more than the drop of fluid in which it is being cultivated —on the other hand, the universe of an astronomer is all that he can observe.

(2) Therefore the universe of every organism is more or less different from that of any other one, for even when we consider two organisms of the same category, or race, the universe of each is not the same as that of the other merely because it includes the other. B is part of the universe of A but A is not in A's universe but in B's.

(3) Every organism has a unique point of view, for all other things are external to it. It is privileged in a sense, being, from its own point of view, the centre of its universe. As it moves forward its universe opens out in front and contracts behind. Its direction of motion is from itself as origin and it makes its own "frame of reference." On the modern theory of relativity all scientific measurements of space and time belong to, and have strict validity only for the observer that makes them and no other observer making measurements of the same things can get absolutely identical results. It is necessary to make certain conventional "reductions" of the measurements in order that they may be valid for the two observers. It is true that such corrections, or reductions, may be very minute ones, but that is because man's power over the things in his universe is relatively very small.

(4) The acquired experience of every organism is its own and is unique. Its memory is its own. No other organism can, except by "sympathy" and "intuition," share in the personal experience of any other one.

(5) The interests of an organism are its own and cannot be shared by any other one. If it is a gregarious animal to that extent it inhibits purely personal urges. When it displays, say, the immensely powerful urge of maternal solicitude for the offspring it is only extending its interests, for it is "its own" offspring for which it may inhibit the urge of individual self-preservation, and not that of other animals.

49. *ON ORGANIC PURPOSE*

We have, in ourselves, the most immediate and certain feeling and knowledge of purpose. The functioning body needs to

assimilate, the need is felt and rises into consciousness as hunger, which becomes desire for food. The urge is then manifested in behaviour, in hunting or in the other more ordinary ways of procuring food. We eat, thus consummating what may be a complex train of anticipatory activities. We may be placed in conditions of personal danger and the urge to self-preservation may manifest itself in deliberated effort—as when the master of a ship makes thought-out preparations for avoiding the risks of an approaching cyclonic storm. We feel the urge of reproduction and that may be the stimulus to activities that are acutely present in consciousness. If there is anything that we are certain about it is that our own conduct expresses motive, or purpose, in the most ordinary senses of those words. And not only are we convinced that other men and women, behaving in the ways that we behave, have the same general motives and purposes that we have, but we are also convinced, from the similarity of *their* behaviour, that hosts of animals also behave with motive, or purpose, and have immediate feeling and knowledge that they do so.

It is when the structure, and the patterns of behaviour exhibited by the lower vertebrates and most of the invertebrate animals differ widely from ours that this extension of our own feelings and motives to them becomes difficult. Partly this is due to our lack of familiarity with the behaviour of these organisms—and it is notable that when the activities of even so primitive an animal as an infusorian are closely studied the less unfamiliar do its activities appear: it has been said that the organism behaves in the way that we do when we say that we act intelligently. Partly the difficulty comes from the attitude that was once held—that animals lower than man were properly to be regarded as automata. Mainly, however, it is the result of too much laboratory training. It has been said that natural history of the old kind is only to be called "science by courtesy." The ascription of purpose to the lower animals was called "anthropomorphism" and was something to be avoided. The tendency to study animal activity in terms of tropisms, taxis, "concatenated" and "conditioned" reflexes and so on was regarded as a much more scientific one!

We can regard an organism as a physico-chemical system. As such it continually tends to chemical degradation and energetic dissipation. Yet it maintains equilibrium, continuing to renew

by assimilation, so much of the parts of its body that undergo waste by reason of their own activities. This organic process is, in a way, the opposite of the degradative and dissipative process that tends to the destruction of the animal system. The latter maintains its " normality " and that maintenance is the result of the life-urges—it expresses life.

The activities that maintain normality need not be conscious ones. We have no reason to believe that the suckling infant has " knowledge " of the complex activities that it carries out. We are unconscious of assimilation, or growth, but " purpose," in the sense of tendency that is opposite to the purely physical ones of tissue katabolism, underlies such functioning. It is in this sense that we may speak of the purpose of the processes that maintain an " artificial " tissue-culture. The purposes may not be such as to warrant our ascribing consciousness to the systems in which they are manifested, but they must be assumed and regarded as something that is, in the wider sense, psychical.

IV. THE LEVELS OF BEHAVIOUR

The motions of animals that we call their behaviour are therefore to be considered as the manifestations of urges, psychical in nature, though they may not rise into consciousness, and having " purpose " in the sense that they are tendential in a direction in which a material-energetic system as such, is not tendential. They operate so as to confer power over the immediate environment. We can consider the behaviours of *all* animals in these terms. But there are many general types of animal structure and innumerable variations of these general types. So also there are as many types and variations, or patterns of behaviour. We shall, quite arbitrarily but conveniently, consider these patterns as falling into various rough levels or grades of complexity. In the more complex grade the behaviour is the more efficient, in the sense that it confers on the animal exhibiting it all the more power over its environment.

50. *ON THE INORGANIC MODEL—SIMPLE RESPONSE*

Let there be a compass needle freely movable on its pivot in a magnetic field. The latter may be that established in the neighbourhood of a bar magnet which can be moved in position.

The field is representable by "lines of force" and the numbers and directions of these are specifiable in any particular experiment. When the bar magnet is moved the whole field becomes changed. The needle will "respond" to the movements of the magnet by changing its inclination to, say, the earth's magnetic meridian at the place of experiment.

But in all this there is simple physical functionality. The whole system, magnet, field of force and compass needle are one, just as is a stretched sheet of some flexible fabric : if one corner of the fabric be pulled the whole sheet becomes distorted. There is complete physical determinism.

Let the charge of explosive in a gun be fired by a detonator which "goes off" when a momentary electric current is passed through a fuse. In such a case the explosion may be called the "response" to the "stimulus" of making contact in the apparatus that transmits the current.

50*a*. The Muscle-nerve Preparation. This is usually the gastrocnemius muscle of the frog's hind leg, with the attached sciatic nerve. When the electrodes from an induction coil are laid on the nerve and when a momentary current is passed through a small part of the latter a nervous impulse is initiated and this is propagated along the nerve into the muscle, where it initiates a momentary contraction. As often as the muscle is thus stimulated it responds by a contraction. By and by the muscle will fail to respond, whether it be stimulated directly, or *via* the nerve—just as a flash-lamp will fail to "respond" to the pressure of the button, by lighting up, when the battery becomes exhausted.

The muscle-nerve preparation, although it is organic in origin, is not an organism. It would be easy to devise a mechanism of artificial nerve and muscle which would do much the same things (though we cannot yet, of course, elaborate a similar mechanism). Such a machine would exhibit "design," but not "purpose" in the sense in which we have used this term. It would be something that does not naturally occur but which had been fabricated, or assembled so as to do certain things. But its activities would tend towards its dissipation, or inability to operate, as in the case of the running-down flash-lamp. Its activities would not tend to the maintenance of its normality, as an organic purpose does.

51. *ON TROPISMS*

A tropism is a growth movement in response to a vector stimulus (which is a stimulus that has direction as well as magnitude). Almost the only good examples of tropisms are the growth movements of plants in response to the light that falls on them, or in response to gravity. The green part of a seedling grows vertically upwards in the direction in which the light falls and the rootlet grows vertically downwards in the direction in which the earth's gravitative force is exerted. The upward growth of the green shoot is called *phototropism* and the downward growth of the rootlet is called *geotropism*. Again, the leaves of a plant placed near to a window tend to turn so that they receive the most favourable (or " optimum ") intensity of light, that is, they turn so that the light may fall normally to their green surfaces. These movements and others of the same type are effected either by the cell-divisions of the growing tissues occurring in planes such that the shoots, or rootlets, or leaf-stems take up certain attitudes, or they are effected by variations in the turgidities of the tissue-cells.

Tropisms have " sign." The phototropism of the growing plant is said to be positive when the growth occurs towards the source of light, negative when the growing plant turns away from the source of light. The sign of the tropism is said to be reversed when a change in the tensor, or magnitude, of the stimulus (the direction of the latter remaining the same) causes the direction of growth to be reversed. There is little precision in these latter ideas, for good examples of tropisms are few.

There is purpose, in the sense used, in a tropism, for the growth movements are such as to promote assimilation. With variations in the direction of the incident light the rate of CO_2-assimilation would sometimes fall off, but given such a change of direction of growth as will maintain this rate constant, or as nearly so as possible, then the tendency of the tropism is to maintain normality. But there is not behaviour in the precise sense which we have adopted, for the plant itself as a whole does not move. There is simply change in the direction of growth of some of its parts relatively to the growth of the other parts.

52. *ON TAXIS*

By taxis, or the tactic movements of animals, is meant movements of the whole animal effected in response to a vector stimulus. Examples are (1) the swimming movements of many larvæ with respect to the direction and intensity of the incident light: a very good example is afforded by opening the shells of Barnacles (*Balanus*) about the end of March and placing the embryos in a saucer of sea water standing near to a lamp. As the larvæ hatch out they swim along the surface of the water towards the light and then away from the light at the bottom of the water. This is *phototaxis*. (2) If a capillary glass tube be filled with a culture of some kinds of aerobic bacilli and then observed beneath the microscope it may be found that the organisms will move towards the open ends, where the oxygen-concentration will be greatest. If the ova and spermatozoa of many marine animals (say those of a flounder) be placed in water the spermatozoa will be seen to move towards, and attach themselves to the ova. These are examples of *chemiotaxis*. (3) If a current of electricity be passed through water containing some kinds of organisms it may be found that the latter will move either with or against the current. This is *galvanotaxis*.

As in the case of tropisms the taxis has sign and this may undergo reversal when the direction of the stimulus changes. And when the tensor of the stimulus changes the sign of the taxis may also change.

Taxis constitutes true behaviour since the activities of the animal, as a whole, are involved. There is also purpose in our sense. For instance, the oxygen-concentration in the capillary tube mentioned above is lowered by the respiration of the bacilli and the assimilation, or other activities of the latter will tend to fall off. Therefore they move to the neighbourhood of the open ends where oxygen is being taken up from the outer medium. Thus normality is maintained. But it does not seem possible to ascribe purpose, in this way, to all so-called tactic behaviour.

52*a*. THE RESOLUTION OF TAXIS. It is possible, in many cases, to explain the mechanism of taxis.

(1) There is a basis of random movements. The animal "fidgets" because it is continually being stimulated by small

unco-ordinated agencies and possibly also because its central nervous system is normally unstable to a slight extent. In the absence of vector stimuli we may therefore suppose animal movements to occur at random. Let there be a " stimulation field," such as a drop of noxious acid in the water in which, say, a Paramœcium is living. Round the drop the intensity of the stimulus decreases in a roughly symmetrical way as the acid diffuses outwards. The Protozoan swims, at random, into this field of stimulation, experiences a noxious effect and changes its direction of motion. Perhaps this change may carry it outside the field, but if it does not do so the animal again turns away and repeats these changes until it avoids the noxious stimulation. A definite behaviour is displayed by a Paramœcium in these cases and, along with its structure, a definite behaviour-pattern, or " avoiding-reaction."

(2) Most higher animals are bilaterally symmetrical, there being similar receptors, say eyes, on the two sides of the body : there are also similar locomotory apparatus, such as wings. Action of the wings on one side of the body will turn the animal to one side in its locomotion. Stimulation of the receptors on one side, but not on the other, may thus be expected to turn the direction of motion to one side or the other. Symmetrical stimulation on both sides may be expected to maintain direct forward locomotion. The classical examples are birds that fly into the lanterns of lighthouses and moths that fly into candle-flames. Such reactions are said to be " forced " ones. Another much-quoted example is that of the caterpillar that climbs vertically up a shrub and feeds on the young and tender shoots. Here phototaxis is said to be associated with the habit. The animal is stimulated optically on both sides of the head so that if it turns to one side the other is more strongly stimulated and the turning aside is thus corrected so that the animal preserves, on the whole, an upward motion. Having fed, it then descends the shrub and we are bound, by our hypothesis of pure taxis, to assume that the changed " physiological state " of the animal, which is consequent on its having fed, changes the sign of the latter so that the caterpillar is now negatively phototactic.

There are also many examples of vertical migrations of Diatoms, Peridinians, micro-crustacea and other planktonic marine organisms. These up-and-down motions are to be

associated with changes in the intensity of light penetrating into the sea—day and night, dull and bright sunlight and the phases of moonlight. Doubtless they are examples of phototactic behaviour, but we know so little of the physiology of the organisms concerned that an explanation, purely on this basis, is apt to be somewhat artificial and formal.

53. *ON REFLEX ACTIONS*

In a case of simple, organic response, as when the isolated frog's muscle is artificially stimulated, either the effector organ, or the nerve going to the latter is directly stimulated. In a reflex act the stimulus is applied to a receptor and then the latter transmits an impulse to its afferent nerve, which impulse stimulates a nerve-centre. An impulse then issues from the centre along an efferent nerve and this, going to an effector organ, stimulates the latter to action. Thus the original stimulus was first thought about as being reflected out from a nervous centre. It will be seen that, in the main, a reflex act is based upon a morphological conception.

Examples of reflexes, in the ordinary sense, are (1) a sneeze, when the stimulus is an irritation of the nasal mucous membrane ; (2) blinking, when the stimulus may be some visual one, suggesting damage to the eyes ; (3) the kicking movements of a hind leg which can be elicited from a dog, lying on his side, when the skin of the flank is lightly tickled ; and (4) the familiar " knee-jerk," which is a kind of reflex. These are trivial examples and do not indicate the importance of the conception—all ordinary behaviour has a basis of reflex actions, which are combined, " concatenated," inhibited, controlled, " conditioned," etc., with the results that we see in animal activity.

The central point for consideration is *the rôle of the nerve-centres in reflex activity*. These centres, in the higher vertebrate animals (which are those that we know well enough to theorize about), are the following :

(1) The grey matter of the central columns of the spinal cord. (The peripheral columns are tracts of nerve-fibres.) This grey matter is primitively segmentally arranged and is still functionally segmental. For each pair of spinal nerves in connection with the cord there is a ganglionic region. (But these overlap.)

(2) The nuclei, or ganglionic centres, in the medulla.

(3) The ganglia of the pons and cerebellum.

(4) The great, primitive basal ganglia of the mid-, and fore-brain.

(5) The grey matter of the cortex cerebri, which covers the cerebral hemispheres.

These nerve-centres form a hierarchy of increasing importance in the order (1) to (5). They are connected by tracts of nerve-fibres and the arrangements of centres and tracts has great anatomical complexity. There are also the following centres in the vertebrate animal:

(6) The diffuse " nerve-net " which exists as the plexuses in the walls of the alimentary canal. (This is very primitive according to a certain morphological hypothesis, not entirely accepted by anatomists, but never confuted. These nerve-nets are what remains, in the higher vertebrates, of the original, or primitive pre-chordate nervous system.)

(7) Ganglionic centres in the heart substance.

(8) The ganglia of the sympathetic nervous system.

53*a*. THE CENTRES IN REFLEX ACTIVITIES. To some extent each centre is autonomous, that is, it can be operative, of itself, in reflex activity.

The nerve-nets. The most finely adjusted reflexes that can be imagined are carried out by the plexuses in the alimentary canal walls (intestine). These are the wave-like movements of peristalsis effected by exactly co-ordinated contractions and relaxations of the transverse and longitudinal muscles of those walls. The centre is the plexus itself.

The heart-centres. The heart muscles contract and relax in most complex and nicely co-ordinated ways under the control of their own ganglia. Heart-movements are controlled from higher (cerebral) centres, but the isolated heart in lower vertebrates will continue, of itself, to beat.

The sympathetic ganglia. These control the working of many glands and the blood-vessels, by themselves (though like the ganglia of the heart, they are also controlled by the brain).

The spinal cord. A very great number and variety of reflexes can be carried out by the spinal cord ganglia. In many lower vertebrates the brain can be completely cut off from the cord

(as in " pithing " a frog), or the head may be severed from the body (as in frogs, insects, etc.) and the animals will continue for a time to live and function. The " spinal " or headless frog will swim, preserve normal posture, wipe off irritants from its body, etc. All such activities are reflexes. They only occur when the receptors of the skin are stimulated. If there is no such external stimulation the frog will exhibit few or no movements. It has no " spontaneity " of behaviour.

The decerebrate animal. The lower mammal (even a dog) can be made " decerebrate " by the gradual removal, by operation, of the entire cortex cerebri, and even much of the underlying, more primitive basal ganglia (corpora striata, etc). Even with such mutilation the animal may live, feed, reproduce, etc. (But, of course, there are limitations to its bodily activities and there are extraordinary emotional modifications.) Here the functional centres are the deep ganglia of the brain, the cerebellum, pons, medulla, cord, etc. These are adequate for a great number of reflexes and the receptors of the latter are the skin and the great sense-organs of the head. The afferent nerves from the cephalic sense-organs do not directly go to the cortex (except in the case of the olfactory receptors) but to the medullary and basal ganglia.

Thus there are numerous nerve-centres in the animal body that are stimulated, *via* afferent nerves coming from receptor organs. These centres then initiate stimuli which are transmitted to the muscles and other effector organs and the latter then move, or secrete, performing reflex activities. Some of these systems of reflex arcs, the intero-ceptors (stimulated by food substances), the nerve-nets and the muscles of the alimentary canal, are practically independent of the rest of the nervous system ; others, such as the arcs pivoting in the heart ganglia, those centering round the respiratory ganglion in the medulla, some of the sympathetic ganglionic arcs, etc., are nearly independent. They carry on regularly automatic reflex-activities, but there is always some control of the latter exerted by the higher brain-centres. Even the movements of the limbs in walking, swimming and other habitual activities are the results of reflexes centering in the ganglionic spinal cord and they may work largely independently of the brain. But there is always potential, or actual, control of them by the brain.

53*b*. THE "INTEGRATIVE ACTION OF THE CENTRAL NERVOUS SYSTEM." Every nerve-centre is in indirect connection with all the receptors, on the one hand, and with all the effector organs, on the other. But each centre is predominantly associated with some limited system of receptors and effectors, that is, certain reflex activities are its characteristic province. Thus there are ganglia, or regions of grey matter in the cord, roughly delimited by the repetitional spinal nerve-roots, and each such region, or segment, has associated with it some region of skin with its receptors, and some group of muscles. (But the demarcation is not precise and the segments overlap.) Similarly the cerebellum is associated with the receptors of the otic labyrinth, with the mechanism of tonus of the skeletal muscles, etc. Nuclei in the brain are associated with the afferent nerves coming from the great receptors of the head. And so on. But while these ordinarily working delimitations exist it is nevertheless the case that any system of receptors can be put in connection with any system of effectors and this is because connecting tracts of nerve-fibres potentially or actually join up all the centres with each other. This is the only general statement we can make as to the extraordinary complexity of the brain and spinal cord. The analogy with a telephonic exchange has often been suggested: it is useful, but must not be laboured. Above all is the cortex cerebri in the higher vertebrates such a mechanism for joining up systems of receptors and effectors *via* itself and the subordinate centres. This is the key to the almost indefinitely great complexity of the mammalian brain.

53*c*. CHARACTERISTICS OF REFLEXES. We approximate to the conception of the "simple reflex" by partially mutilating the experimental animal. Thus the brain of the frog is destroyed so that activities pivot on the spinal cord, or the cerebral hemispheres are wholly or partially removed so that it is the cord and the lower brain that are the centres, or the cord may be cut through so that segments, or groups of such, are the centres for the reflexes. Mostly the latter are studied in mutilated animals so as to simplify the phenomena to be observed.

(1) In the most simple cases, as in the spinal frog, the reflex is nearly "inevitable." That is, given the stimuli and freedom from control by the higher centres, the effect nearly always occurs and nearly always in the same way. (2) It is "all or

nothing" with a reflex. There is a stimulus of a certain minimal intensity and if below this intensity it will not lead to effect. If it has effect it is the full effect. There are gradations of strength in, say, the muscular act that follows a stimulus, but these are consequent on more or fewer of the fibres in the nerve, or muscle, being stimulated. (3) There is a "refractory period" following the stimulation of a nerve and during this another stimulus does not act. (4) There is "fatigue" in the reflex, but this is in the synapses, or in the substances adjacent to the end-organs in the muscles. (5) There are "facilitation" and "induction" in reflexes, that is, one stimulus may reinforce another one and one subliminal stimulus following another in the same field of receptors may have effect. (6) There is "exaltation" of effect following an inhibition of a reflex. (7) The effect of stimulating a nerve depends on the ending of the nerve in the effector organ. And so on.

Chained Reflexes. In the intact animal there are chains of reflexes, the effect of one being the stimulus for the next, and so on. Thus the successive contractions of the œsophagus in swallowing; the writhing locomotion of the foot of a snail, or the successive action of the segments of an earthworm, etc., or the stimulus of seeing a fly causes the frog to dart out its tongue and catch the insect, when contact of the latter with the mucous membrane of the mouth causes the latter to close, which is the stimulus for the swallowing movements of the gullet.

Combining of reflexes. Thus antagonistic muscles are stimulated in succession, or the stimulus to contraction of the muscle that bends a limb is simultaneous with the stimulus to relaxation of the antagonistic muscle that straightens the same limb. And in complex activities the reflexes are initiated and co-ordinated in ways that are beyond analysis except in simple cases.

And it will easily be seen that all the mechanism indicated in the above sections do not, in the least, explain behaviour: they are only analyses of the means of behaviour. How activities are adjusted to the circumstances is our problem, and it is obviously a psychical one.

53*d*. The Purposes of Reflexes. Just as easily do we see that all the reflexes that can be studied have purpose, in the sense of the term adopted. The scratch reflex of the dog is

such an activity as tends to remove irritants (say fleas); the movement of the spinal frog in wiping off a drop of acid has the same significance; the secretion of saliva when a dog is shown meat is anticipatory to eating, swallowing and assimilation. An antagonistic reflex has purpose in that the co-ordinated activities of the two muscles more efficiently moves the limb than would one muscle simply overcoming the other. In short, it will be found, on analysis of the activities of any reflex in an unmutilated animal, that normality is the result of the act, or the urges of life are in some way satisfied by it. This is its "purpose."

And it is always necessary to remember that in speaking of "a reflex action" we are arbitrarily and conveniently focusing attention on one aspect of bodily activity. There is no "simple" or unitary reflex act in normal behaviour. What appears to be such is merely due to our necessary restriction of attention. All the body is involved in every behaviouristic activity that we see and our insistence on the rôle of reflexes merely aids in our analysis of that activity.

54. *ON ACTION*

By action is meant animal behaviour that has a basis in "trial and error" but which is controlled by experience. Nearly all the normal behaviour of unmutilated animals that are placed in "average" environments, and receive ordinary stimuli are actions in this sense. The latter qualifications appear to be necessary in order to exclude "forced" activities from the field of actions—thus the flying of moths into naked flames, the flight of birds into the lanterns of lighthouses, and perhaps other activities are to be regarded as "purposeless," that is, they do not tend to self-preservation, or to other life-urges and they appear to be responses to stimuli that are so powerful as to inhibit the integrative tendency of the central nervous system.

54*a*. ORGANIC EXPERIENCE. The events which happen in the system of things that includes an animal organism affect and modify the psychical and physical mechanisms of behaviour. This is what is meant by "experience." There is no purely inanimate analogy to this. It is true that physical, lifeless things are affected by the events in which they participate: thus a razor-edge becomes blunted by use; a clock-spring

becomes less elastic, a thermionic valve "loses its emission," and so on, but the proper analogy with these phenomena are the "senile decay," or the bodily accidents of an animal and not the changes in its modes of behaviour. The changes undergone by the physical systems are manifestations of the physical and chemical degradations expressed by the entropy law and they tend to the loss of the particular "properties" of the systems. On the other hand, the experience of an animal tends to make its behaviour more efficient and purposeful—that is, the better to satisfy the needs and desires implied in the urges of life.

Causality and experience. The causality included in a physical system is measured by the quantity of available energy, but this need not be the case when the system includes an organism. Thus CO_2, OH_2 and some other simple mineral substances, with solar radiation make up a system in which the available energy (or sunlight) simply dissipates. But let the system include a green plant and carbohydrate is formed, when available energy, or causality, is conserved. The system may be CO_2, OH_2, etc., with the energy from a quartz mercury-vapour lamp, glass vessels and an experimental chemist. Such systems existed in the nineteenth century, but they did not synthesize carbohydrate. But at the present time chemists "of experience" can so assemble the apparatus as to couple together energy-transformations and bring about the syntheses. The latter are still very imperfect—that is, the "yield" of sugar in any experiment is small, but we have no doubt that additional "experience" will tend to increase this "yield." Thus there is physical causality measurable by the available energy of the system considered and there is also organic causality which is inherent in the behaviour of some animal which is associated with physical things. This causality, or skill, or efficiency of behaviour is not diminished by use and it can be communicated without diminution. It increases by individual acquirement—thus all good artisans, surgeons, etc., become more skilful, that is, become centres of increased causality. This increase of causality, due to their greater power over the things in their environment, is their organic experience.

The "Retention of the past." The past is said (in a loose kind of way) to "survive," or partially to be retained in an

animal, as pure memory, as motor habit, as individual acquirement, as instinct and perhaps as heredity.

Pure memory is the retention in present consciousness of past states of consciousness. "Past" means here the immediate intuition of duration and is not "the physical past." (In the passage of nature entropy increases, so that of two events that one which displayed the lesser entropy was the "physically" past one.) The retention of past states of consciousness is incomplete and ultimately fails as the animal becomes senile. We call it memory, the imagination of past things, visualization of past things and so on. It is elementary and indefinable.

Motor-habit means that behaviouristic activities acquired with difficulty become facile, or habitual, are performed automatically and may become *instinctive* in the offspring of the animal in which they were acquired. These matters we shall examine more closely in the further sections.

54*b*. TRIAL, ERROR AND EXPERIENCE. Behaviour that merely involves random acts that are tried again and again until one is successful is probably exceptional among animals. It may be realized in the avoiding-reaction of Paramœcium (Section 52*a*) or by such behaviour as that of a Vorticella upon which a stream of particles is allowed to fall. The animal may respond, first by a reversal of its ciliary motion, then by bending to one side or the other and finally, should the previous trials fail to avoid the irritant, by breaking its stem and swimming away. If such experiments are repeated many times on the same individuals, and if there is always the same sequence of trials, there is no action, in our sense of the term.

The labyrinth experiments are typical of a large class that demonstrate experience. The animal is placed near food which it can smell but which it can apparently approach by several alternative paths, only one of which, however, enables it to obtain the food. It will try the various paths at random, finally traversing that one which is successful. If now the same experiment is repeated many times with the same animal and if the latter finally chooses the right path at once, there is true action. Many variants of such an experiment have been made with much the same results and apart from academic evidence ordinary observation leads to the same conclusions: thus a man in a

town that is strange to him will at first find his way from one point to another by trials, but very soon he will discover the shortest route. Obviously dogs and carrier pigeons will do much the same thing, and so on.

"*Conditioned Reflexes*" demonstrate experience as it affects organic functioning and behaviour. A dog, for instance, is given food at the same time, or slightly after a whistle, or some other signal. The dog salivates while he eats the food. After many repetitions of the signal and the feeding the dog will salivate when the signal alone is made. This is a reflex to a stimulus which did not of itself originally evoke response but which acquired significance from its association with food—that is, by the experience of the animal. Again, ordinary observation will show the same result—the dog knows the dinner bell. The normal dog, will, of course, salivate when shown food and, after some training, when food is spoken about. But it is easy to see that the normal unmutilated dog can be "fooled"—when his behaviour to a signal may change. The "conditioned" reflex is said to be "inhibited."

The historical basis of acting. In all these cases of behaviour that becomes more efficient by repetition there is a history of events that were anticipatory to the "finished" behaviour. Some satisfactory response to external conditions becomes established in the behaviour of an animal. A stimulus is received and then the animal responds by some train of actions which we proceed to analyse. We see clearly in ordinary behaviour that the activity cannot be simply a response in the sense that a "decerebrate frog" will (for instance) croak inevitably when its body is stroked in a certain way: what we call the stimulus in ordinary behaviour is far more complex than this and it is not simply some physical events in the environment. Thus to a bilingual person a sentence in French is an entirely different physical stimulus from one in German, but the two sentences may evoke precisely the same behaviour. When Mark Twain was learning German the word "damit" satisfied a certain need, but when he came fully to understand its meaning it, as a stimulus to behaviour, became "conditioned" and no longer led to the same response. A physical stimulus *acquires meaning* when it has become associated in memory, or in motor habit, with certain other stimuli and responses.

Reflection on one's own behaviour and observation of that of animals that one knows well will amply demonstrate this.

54*c*. The Establishment of a Motor Habit. Such actions as these: the spinning of a web by a spider; the building of a nest by a bird; swimming by a boy; the rapid building of a wall by a bricklayer, etc., all involve the establishment of motor-habits. They are series of bodily actions that may be performed efficiently and automatically. Each involves trains of accurately adjusted, co-ordinated and chained reflexes such that the completion of one series of acts is seen, felt, etc., and is the stimulus that initiates the succeeding acts (just as in organic functioning the contraction of one segment of the alimentary canal is the stimulus for the contraction of the succeeding segment, or peristalsis). The physiological basis of this motor-habit establishment is the laying down of a *neurone-pattern.*

Neurone-patterns. If we "blink" with the eyes there is some visual stimulus, with noxious meaning, that affects the retinal receptors. This stimulates the optic nerves, which are connected, *via* synapses, with fibres that stimulate the synapses in the centres, or nuclei, of the motor nerves of the eyelids. These latter muscles are finally stimulated and we "blink." Thus the reflex uses, as a mechanism, a particular chain of neurones, among very many other chains that are all possible ones. The chain involved in blinking-behaviour is a neurone-pattern. How neurone-patterns are set up we can only "explain" by the random conception. Many possible trains of neuro-muscular activity may follow a stimulus (because of the exceeding complexity of the synaptic nervous system.) In the initiation of a motor habit many such trains are certainly "tried" and one proves to be successful—that is, is instrumental in behaviour that satisfies a need, averts a danger and so on. This train is afterwards adopted by the animal, without initiatory trials, when a stimulus having the original meaning is received. But the essence of the explanation is this—how does the successful response become adopted, or selected, from among all the possible ones? The answer is impossible on ordinary physical grounds. The adoption of the neurone-pattern means selection—that is, something opposed to randomness and psychical in nature. Apart altogether from laboratory experiments introspection with regard to our own behaviour and observation of

the activities of other human beings and of many non-human animals show all this quite clearly. We are very familiar with "aimless," "purposeless," "desultory" behaviour in other people and sometimes oppressed with our own disinclination to sustained effort. We are often annoyed by the inability of a dog to do what we want it to do. Something is common to all these kinds of behaviour—the randomness of the chains of reflexes that occur and the absence of definite choice of neurone-patterns.

54*d*. Intelligence and Instinct. The methods of behaviour by trial and error, with the acquired basis of historical action constitute intelligence. In man this rises to the plane of rational activity, when we have to deal with the conception of "excess-value" (see the following sections). When we come to consider *instinct* the analyses of motives, purposes, establishment of motor habits, memory and "subconscious" memory all follow along the lines already indicated. So far as the limitations of space permit we have discussed intelligence and little need be said about instinct.

An instinctive activity is one that is purposeful, has not to be "learned," or acquired by the individual animal that performs it, and which is efficiently carried out the first time that it is attempted. It is innate in the organization of the individual. The swimming of a dog, the building of a nest by a stickleback, the choice of an empty gastropod shell by a hermit-crab larva, the suckling actions of the human infant, the gripping movements of the hands, etc., are all instinctive activities. The problem that we encounter in dealing with such kinds of behaviour is not their origins, for these may be explained just as we have indicated in the cases of intelligent activities. What is really troublesome is the question of the transmission of action so that things that are learned, or acquired by the individual, can be done also, without being re-acquired in the same ways, by the offspring of that individual. That is, some kinds of behaviour may originate and be "transmitted" by heredity. Instincts, in short, are "mutations" of behaviour, just as there are mutations of structure and functioning, and the discussions that follow in sections with regard to the latter phenomena appear to apply also to the transmissibility of instincts. That is all that need be said about the problem in the present place.

V. EXCESS-VALUE IN BEHAVIOUR

By excess-value in behaviour is meant those degrees of activities that *do more than* satisfy the urges of assimilation, growth and reproduction, and self-preservation. By "values" is meant simply measurable estimates of the activities in question.

A candid survey of the behaviour of men and women, and even of many of the other animals, will show that the treatment of the early part of this chapter affords only a most inadequate description of those organic activities considered. We have, therefore, to attempt an extension of the conceptions already made in the hope that some results of greater applicability may be obtained.

55. ON NORMALITY IN ORGANIC ACTIVITY

The inorganic model illustrating this conception is the activity of an acid. Such a substance tends not to occur freely in nature since it exhibits a tendency to become *neutralized* by one or more of the chemical substances called bases. In proportion as neutralization proceeds the characteristic tendency of the acid decreases. When it is completely neutralized a salt is formed and this is a more stable substance than an acid. Thus the tendency is for all siliceous (acidic) minerals in the crust of the earth to combine with the basic ones, to the extent that the latter are present.

The blood of a vertebrate animal has a certain normal constitution, such that its hydrogen-ion-concentration, its O_2-content, its CO_2-content, etc., remain as nearly as possible constant. The H-ion concentration is actually very nearly constant (or "normal") in the healthy animal. The proportions of O_2 and CO_2 vary within certain limits, but the integrative action of the nervous system, *via* the respiratory organs, tends always to restore the O_2-content should this fall below normality, or to diminish the CO_2-content, should this rise above normality. The tendency, then, of the tissues of the animal to retain a certain normality is satisfied by various regulatory mechanisms *which cease to operate when the normality is attained.*

56. *ON THE EXCESS-VALUES OF THE URGES OF LIFE*

The results of animal behaviour are often in excess of those that are necessary for normality. This we consider more in detail.

i. Assimilation. The expenditure of energy by the animal depletes its tissues of oxidizable material. If it grows or reproduces this depletion is again the case. Therefore there must be continual assimilation of materials into the body. This necessitates the behaviour of obtaining, and eating food. There is an urge to assimilate which is felt as hunger and eating satisfies that urge. Normality would be attained when just so much food as would provide for the necessary assimilation is ingested, but as a rule an animal which is hungry will eat more than this and may fatten (to its disadvantage), or may merely excrete the excess of foodstuffs eaten. In the healthy animal that is of constant weight and in nitrogenous equilibrium there is normality as regards assimilation. Of itself, however, the animal may "over-eat" because of the pleasure of doing so. This is excess-value of assimilation. In civilized man it is represented by the banquet, etc.

ii. Growth. Excess is represented by corpulence, or in a sinister quality by the malignant tumour.

iii. Reproduction. Normality may be taken as given by that density of individuals, in any region, which is constant—when, on the average, as many are born and live to reproductive age, as there are deaths. Actually there may be an enormous preponderance of births over the deaths of reproductively mature individuals (and there will, of course, be a correspondingly high death-rate of individuals that never became reproductively mature). This is excess-value of reproduction.

iv. Reproductive Behaviour. Both in man and the higher mammals and birds there is complex behaviour anticipatory of the essential reproductive act—which is the conjugation of the gametes. This behaviour is now an extraordinarily large part of general human activity—that is, it has marked excess-value. It is represented by "lover's poetry," erotic, and much "romantic" literature, prostitution, sexual perversion, etc.

v. Self-preservation. Normality is, perhaps, represented by

the survival to the phase of reproductive maturity of a population adjusted in density to the natural productivity of a region. In human populations, of course, invention has enormously increased both productivity and density, but there is a limit in all cases. Beyond this limit there is over-population, which is the result, not only of excess-value of reproduction but also of self-preservation as it is expressed in preventive medicine, public sanitation, "safety first," etc. The effect of excess-value of essential reproduction is minimized by birth-control (artificial and natural), though along with this non-essential reproductive behaviour may continue to exhibit enormous excess-value. The manifestations, in man, of excess-value of the urge to self-preservation are illustrated by:

The elixir of life; sex-gland therapy; Swift's monstrous fable of the Struldbrugs, etc.

Shelter. The elaboration of the burrow, nest, hive, etc., in the lower animals; the humanly constructed house, palace, etc. Here there is obviously enormous excess of the essential conditions of shelter from inclement nature.

Dress. Clothing is essentially protection against inclement nature, but even among savage peoples the protection receives enormous over-elaboration and ornamentation—far in excess of utility.

Weapons. The damascening of a sword-blade or the jewelling of the hilt.

Transport. The restaurants, ball-rooms and swimming baths of an ocean-liner.

Language, and writing, etc. "Culture" in general; the "refined voice," exclusive accent, etc. And so on to an extent easily explored by the student.

Plainly these illustrations indicate that the behaviour that originally satisfies an urge may come to exceed the motive. A certain amount, or value, of the particular behaviour satisfies the urge—*as we have, so far, described the latter.* But the mode of behaving now becomes a motive in itself—thus there is an urge to eat nice things apart from the requirements of assimilation. Behaviour, itself, has created new needs and desires.

57. *ON SUBLIMATION*

It is desirable to extend the meaning of this term: by it is meant that the manifestations of an urge have acquired, in the process of evolution, new motives. The matter of this section applies particularly to man.

57*a*. Pleasure and Pain. These feelings are to be associated with the conception of normality. A need that is satisfied is no longer felt, having led, through appropriate behaviour, to normality. In the latter state there is incipient pleasure, which becomes heightened by excess of the behaviour that led to normality. To evoke this pleasure now becomes an additional motive of behaviour (over-eating, prostitution, etc.). The failure to satisfy the primitive urge implies dissatisfaction, and *unavailing* functional or behaviouristic activity implies abnormality, deepening in consciousness into pain. There is the additional motive, in behaviour, to avoid dissatisfaction and pain. Normality thus sublimes into pleasure.

57*b*. Animal Play. Play is plainly anticipatory behaviour carried out by the immature animal and modelling those activities which it will carry out when it becomes mature. It can be analysed so as to display fighting, pursuing, flight with the motives of self-preservation; hunting and killing with the motive of nutrition; fabrication of things by the human child; the making of shelters; maternity, etc. It is amplified, but not initiated, in all animals, by imitation and instruction by the elders. Sport in adult men and women is play that is rationalized. Killing for sport and cruelty in sport are clearly excess-value of the satisfaction obtained by the obtaining of food. Joy in sport is the sublimation of the satisfaction of the urges upon which the play, or sport, is based. Games involving skill can be analysed, as to motives and origins, in the same general way. Games involving chance imply the property instinct.

57*c*. The Property-"instinct," or Urge; the Gregarious Urge. These urges are manifested in the behaviour of the lower animals. Hoarding food, for instance, clearly leads to behaviour similar to ours with regard to property and the gregarious herd, or pack, clearly anticipates the human community. On the one hand, the property-urge sublimates into the group of motives that we call "love of country,"

"patriotism," etc. A man's possessions have come in the course of evolution to include his family, serfs, vassals, dependants, tenantry, etc., and in the long run all that stands for his nation or "empire" with the associated customs and traditions. On the other hand, the property, or acquisitive urge, leads to pure ownership, wealth, control of things in general, the miser, "laissez-faire," "cash-payment," dividends and rents and capitalistic production. Capital is clearly an operation and a little reflection will enable the student easily to regard it as *the monopoly of the means of effecting energy-transformations.* In modern communities the gregarious urge is in conflict with individualism—that is, the expressions of the primitive life-urges and the secondary acquisitiveness of modern man.

58. *ON TRUTH, GOODNESS AND BEAUTY*

Clearly we deal here with sublimations of primitive modes of behaviour and their motives.

Truth was in its inception the correspondence between behaviour and its results. Something that was done *availed* in giving power over inanimate nature and was seen always to avail—some operations were constantly *valid* ones. That three straight lines of 3, 4 and 5 units of length, joined at their ends enabled a builder to mark off the corner of a square (a right angle) was such a continually valid operation. Thinking about it led to the geometry of Euclid I, 47, a result expressing sublimation. Thinking led to other analogous experiences that gave satisfaction subliming into abstract truth. All such results have a basis of validity in obtaining power over nature: thus the equation $pq - qp = ih/\pi$, though no one really "understands" it, expresses a mental operation to which we endeavour to give a "physical meaning." "Knowledge is power."

Goodness means (from the naïve, biological standpoint) the inhibitions of the primitive urges. We obviously beg the question as to whether or not human nature is innately "good"—since *that* problem is not a biological one. Kant seems to suggest that human nature is, in itself "bad," that is, simply expresses the primitive urges, which are individual ones. Evolution in one way has made it "worse" since there has been sublimation of these urges (in acquisitiveness, cruelty, reproductive excess).

With the evolution of the secondary gregarious urge the inhibitions on individual behaviour originated. What an animal might do for itself were no longer its sole motives since it tended also to behave in the interests of the community. Activities that might be advantageous to itself were not of advantage to the community and *vice versa*. Thus the new urges, " ought to " and " ought not to," developed. The inhibitions (so far as man is concerned) were most clearly indicated in the monastic vows of chastity, poverty and obedience. Purely physiological observations tend to support these conceptions. In Goltz's well-known experiments dogs (which are animals with well-developed communal urge) were made decerebrate, when the inhibitory activity of the higher nervous centres was made impossible. In this state they might behave with much of what we have called normality, but their responses to stimuli tended to display what we call " badness "—they would growl, bite and exhibit displeasure and anger, but not such behaviour as would suggest affection. That is, " natural " modes of activity had become inhibited by the gregarious and " domestic " habits of the animals but were again apparent when the mental and anatomical machinery of that inhibition had been destroyed.

Mental conflict. " Insanity " may be actual anatomical abnormality resulting in the destruction of physical mechanisms involving nervous centres and tracts. Perhaps also there is abnormality of the mental operators, but to the conflict between the primitive urges of self-preservation, individual nutrition, and reproduction, on the one hand, and the inhibitions imposed on behaviour by the communal urge, on the other hand, we may trace mental aberration and distress.

Beauty. Perhaps we may assume that the feeling of beauty in natural things is elementary and not to be traced to any more general feeling. Still very much of what we usually call " the beautiful " is better to be called " elegance " and is to be traced back to excess-value in fabrication. Thus a house might be simply a rectangular stone box provided with apertures closed by valves (doors and windows). It might be well ventilated and warmed and, as such, would be a highly efficient shelter. The motive in constructing a house is to provide such a shelter, nevertheless there is much more in the good, modern house than this. So also with dress, with weapons, tools and all the

artifacts that man makes. (We ignore, of course, the baseness of much of the artifacts resulting from modern "mass-production," where the motive is fabrication for profit as well as, and perhaps rather than, for use.) The house, dress, weapon, tool, etc., has purpose and is designed to do something and there is satisfaction in the adaptation, by fabrication, of the thing to its purpose. Plainly, however, the amount of fabrication exceeds that necessary for mere utility and we call the excess-product elegant, or ornamental. The satisfaction of the adaptation and fabrication thus clearly sublimes into the feeling of elegance which is, at least, a large ingredient in all beautiful things made by man.

PART II

THE RACE

CHAPTER V

REPRODUCTION AND GROWTH

I GROWTH

By *growth* we mean that a thing increases in size while still retaining its individuality, or identity.

If it changes in some ways it might become another thing: thus a glacier melts away when it creeps down below a certain level; its stones form a terminal moraine and its ice becomes a river.

In growing the thing must remain the same thing and by this identity throughout an interval of time we mean that the thing remains accessible to our observation, and may be observed continuously, even if we do not so continue to observe it. It maintains a certain essential form and certain essential relations to other things, this essential form and relations being stated in the definition of the thing even although both the form and the relations may display unessential changes. Thus our bodies are, in a sense, continuous things, identical from moment to moment and always under our observation. They grow and change, but while the growth and change proceed they are still our bodies. Other natural things we regard in the same way.

By *simple growth* we mean that a thing increases in size while still retaining its form. Thus a hollow elastic ball that is being inflated with air increases in size, but it still preserves the form of a spherical body. We must regard such simple growth as quite exceptional, for most growing things change in ways that alter their forms. Absolute retention of form while a thing increases in magnitude must be regarded as logically possible. Thus a mathematical function retains its form while its argument changes, but we have excluded such constructions from our category of natural things. Simple growth, then, is a "limiting process" to which actual processes may approximate.

By growth with differentiation we mean that a thing increases in size, retains its individuality and identity but changes in form. In this case the changes in form are included in the definition

of the thing. The best example is that of the development of an animal body. Thus a chick grows from an egg, but the form of the undeveloped egg containing a blastoderm is very different from that of the 6-days' old embryo, which again is different from the newly hatched fœtus. Yet here there is something that remains the same in all these complex changes, and this we call the "organization" of the animal.

Growth with differentiation is the process that we usually observe.

59. *ON GROWTH IN INANIMATE THINGS*

Inanimate things grow by accretion of materials. Some natural process leads to the formation of a thing and then to the increase of this thing by continued process. Thus a river delta forms when a river current becomes great enough to carry sand and mud in suspension. As the river enters the sea the velocity of its flow decreases and the suspended materials are deposited on the bottom. The conditions are such that these deposited materials are laid down as a thick sheet, narrow where the river current begins to slacken and wide towards the sea. The accretion of materials continues and so the delta grows while still retaining its general form of a great, flat, expanse of sand and mud and swamp, roughly triangular in shape. The precise shape varies as the river channels change and as the suspended materials may change, still the delta remains the same thing, being the result of certain natural processes which continue. Its changes of form are "accidental," in the sense that they are due to small, and generally independent causes which are, so to speak, "embroideries" upon the main essential process.

A sand-bank forms in a somewhat similar manner and undergoes growth, with accidental changes in form. A volcanic cone grows with the deposition, on its sides, of materials ejected from the crater. These materials assume a certain "angle of repose" which depends on their nature. The crater may collapse when there are violent eruptions and heavy lava outflows and the form of the cone may become irregular. Still it increases in size and retains a certain individuality, so that we speak, for instance, of Vesuvius as being the same volcanic mountain now that it was when the cities of the Plain were destroyed.

Other cases of natural, inanimate growth may be analysed in the same way. Prominent features are the accretion of materials and the condition that in growth of this kind the materials added to the growing thing are similar to those that make up the thing.

59*a*. CRYSTAL GROWTH. This process we must examine in detail because of the analogy, which has often been suggested, between it and organic growth. A crystal grows in size when it is placed in a strong solution of the same substance as that of which it is composed (or exceptionally of some other chemical substance which crystallizes in the same geometrical form). If certain precautions are taken the crystal that grows in the mother-liquor preserves its geometrical form very closely. As a rule, irregular masses of crystals form and there may be apparent deviations from the typical form, but growth may be so regulated that a small crystal grows to be a giant one which has almost exactly the same arrangement of faces and angles.

The materials of the crystal are the same as are the materials in the mother-liquor. In the latter there are molecules of the chemical substance and these have certain very definite forms and orientations. When they leave the liquid state and become added (by accretion) to the growing crystal they take up definite relations to the parts of the latter. Molecules do not exist, as such, in the solid crystal, for the latter is a lattice in three dimensions and is one thing, but the molecules that become added to the existing lattice are added on in a certain invariable way, so that the new parts of the crystal are similar to the old ones and, in fact, form a continuous structure that has no internal divisions or boundaries.

Organic growth is quite different from this process.

60. *ON ORGANIC GROWTH*

Inanimate things usually grow by accretion of material to their external parts—thus the sand-bank grows by the deposition of materials to its margins and surface. This is sometimes regarded as a distinction between inanimate and organic growth : organisms are said to grow by " intussusception," that is by the addition of materials to their internal parts. But a small block of dry gelatine that is placed in water will increase in size by the addition of water to the internal parts, into which the liquid soaks.

Organisms grow by selecting materials from their media and by reassembling these into the materials of the tissues of their bodies. It is difficult (and perhaps impossible) to find an analogy to this process among inanimate things.

Thus a plant grows by taking CO_2 from the air and water and mineral salts from the soil. It reassembles, chemically, these substances as carbohydrate, fats and proteins and it further assembles these synthesized substances as wood-vessels, leaves, buds, etc. The materials that are added, in growth, to the body of an organism are therefore different from the materials that are present in the medium. By " materials " we mean, of course, the chemical compounds, for the chemical elements in the organic body existed in, and were taken from the environing media.

60*a*. Simple Organic Growth. For a short interval in the life of an animal growth is apparently simple. Thus a boy of about 18 years of age may grow for several years in such a way that all the proportions of the body and limbs may remain almost the same, nevertheless his height and weight may increase. In such a case the body grows while retaining the same form. The growth has occurred after the period of tissue and organic differentiation.

60*b*. Organic Growth with Differentiation. In general the growth of an organism is accompanied by differentiation. Beginning with the fertilized ovum the embryo increases in size, but as it increases there occurs an increasing complexity of its parts. The organ-rudiments form and then the tissues take on their definite structures. The external form of the body may change in a most striking way—even by a definite " metamorphosis," as in the case of the transformation of the tadpole into the little frog. Even when the growth occurs in a direct way, as in the case of man, the proportions of head, trunk and limbs change rapidly during the juvenescent phase of individual life.

Therefore organic growth is what we shall study, later on, as development. In this process an internal agency remains the same in all phases of life, but this agency—which is called the " specific organization "—acts in such a way that the growing body passes through a series of marked changes, or differentiations. If we knew only the tadpole and the fully developed little frog but were quite ignorant of the future of the tadpole and of the past of the

frog, we should certainly say that these two things were distinct kinds of animals. As it is we know, from continued observation, that they are the same animal.

Normal, ordinary organic growth then resolves itself into the study of development.

60*c*. ORGANIC REPAIR AND REGENERATION. Growth exhibits itself in the processes of repair and regeneration. A wound normally heals in such a way that the former structure of the injured parts is restored. The injured tissues grow, but they differentiate at the same time, for examination of the " proud flesh " in a wound shows that this has not the structure of the tissues that are going to be repaired. As the cavity of the wound fills up, however, the proud flesh (granulation tissue) takes on the forms of the muscles, blood-vessels, bone, etc., that were injured and these new tissues arrange themselves in those ways in which the former tissues were arranged before the injury occurred.

Therefore the parts of the body that grew in order to repair damage caused by the accident contained the agency called the organization. This operated by taking chemical materials from the blood, by chemically changing these materials and by rearranging the changed materials in a structure of connective tissue, muscle, blood-vessels, etc. The plan of this structure was in the organization, in the sense that the latter operated in such a way as to realize it.

60*d*. REGENERATION is repair on the large scale. The power of repair exhibited by a complex animal, such as man, is very limited. Wounds, in the ordinary sense, can heal up, but an extensive part of the body, such as a leg, that is destroyed by accident, cannot be replaced. In the structurally simpler animals, such as crustacea, this extensive power of repair is possessed. When a crab loses a limb by accident (or voluntarily, by the curious process called " autotomy ") a little " bud " forms at the stump of the lost limb. This grows and the growing parts differentiate in such a way as to re-form the lost limb. Here the organization can effect far greater changes than it can in the case of the structurally more complex mammalian animal.

60*e*. MALIGNANT, OR SINISTER GROWTH. A form of growth that is called " malignant " is exhibited by those structures called " tumours," " cancers," etc. In such structures, things that " ought not " to be there are present in the body of an animal.

" Wens " are called " benign " growths by pathologists in distinction to sarcomas, carcinomas, epitheliomas, etc., which are called " malignant growths." But in all such tumours something of the same kind occurs : parts of the body—connective tissue, fatty tissue, muscular tissue of the skin, or of a gland, etc., begin to grow, " on their own," and without any correlation with the growth of adjacent parts, or tissues. Thus an obvious swelling, growth, or enlargement of a localized part of the body occurs. If this tumour becomes circumscribed, isolated, or enclosed by a capsule, or other bounding structure, the growth-process may be arrested—then the pathologists call the process " benign." If there is no such isolating capsule, and the growing tumour can spread into (or " infiltrate ") adjacent parts of the body, the growth is called malignant (and " sarcomatous," " carcinomatous," etc. according to the kind of tissue in which it began).

" *Sinister growth* " is the term that may be applied to both the benign and the malignant growths, or tumours, of the pathologists. In such structure the *tissue organization* is present, that is, any part of the body has the power of selecting materials from the nutritive fluids and of arranging these materials in the form that it possesses. Thus connective tissue, that grows in the sinister mode forms only connective tissue, muscle forms only muscle and so on. But the specific organization is wanting, or is rendered inoperative, for the arranging power is not displayed. The limb-bud in a regenerating crab, for instance, exhibits specific organization, for it not only forms connective tissue, but it also forms muscle, blood-vessels, skin, etc., and arranges all these tissues in the form of a limb of a crab. The sinister growth goes on independently (or nearly so) of the adjacent parts of the body, or of the body as a whole, and it may grow in such a way as to destroy the body in which it was included.

61. *ON ORGANIC GROWTH AS A FUNDAMENTAL LIFE ACTIVITY*

Growth is the most fundamental, or irreducible, or elementary manifestation of life. It presents itself in two aspects : (*i*) *Growth that is ordered* and expressed in living things that are, to some extent, tolerant of many other living things. Competition in wild nature obscures, or modifies, this tendency, but its clear manifestations are seen in the evolution of animal communities, especially

in man. (*ii*) *There is sinister or " evil " growth* and this is best manifested in conditions such as we see in cancers, in bacterial cultures, in the riotous disorderly growth of a tropical jungle, or in a seething mass of maggots, infesting some organic substance.

In such conditions growth has, to us, some strongly repellent aspect and in searching for the roots of this feeling we find them in a kind of intolerance, a destructive tendency, a want of order of some kind. Life here expresses itself merely as the insistent effort to make inorganic matter alive. It is, in some way, life that is more elementary than the life of the higher organism—it is life that may have been more characteristic of a former phase of the passage of nature than life is, as we know it, at the present time.

62. *ON THE MEANS OF GROWTH : CELL-DIVISION*

Growth in the organic body may be a simple process of accretion. Thus bone in an animal may consist largely of calcareous material deposited round itself by a living bone-cell, and so with many other growth-processes both in plants and animals. But organic growth in all the multicellular organisms involves the process of cell-multiplication. The bodies of all higher organisms are structures formed by cells and these units have certain limiting sizes which are always very small relatively to the size of the organism. Whatever the nature of the latter, the order of size of the component cells is much about the same. Therefore the mass of the body of an organism is, in general, proportional to the number of the constituent cell-units and in growing the numbers of cells increase.

62*a*. CELL-DIVISION.

i. The gross aspects. The cell displays a constriction so that it comes to have the appearance of an hour-glass. The constriction becomes fine and then breaks so that one " parent-cell " becomes two " daughter-cells." Each of the latter has at first one-half of the mass of the " parent-cell," but it grows (by assembling materials absorbed from the nutritive medium) and, as it grows, its structure differentiates again so that it becomes similar to the " parent-cell." Each " daughter-cell " again redivides, grows and differentiates in the same way until the number

of cells becomes sufficient for the body, or bodily part, or tissue that is growing.

ii. The finer aspects : Mitosis. The cell is a complex of parts.

It is convenient to orientate it so as to indicate " equatorial " and " polar " regions. In it there is a rounded body—the *nucleus*, which is bounded by a *nuclear membrane*. The substance of the

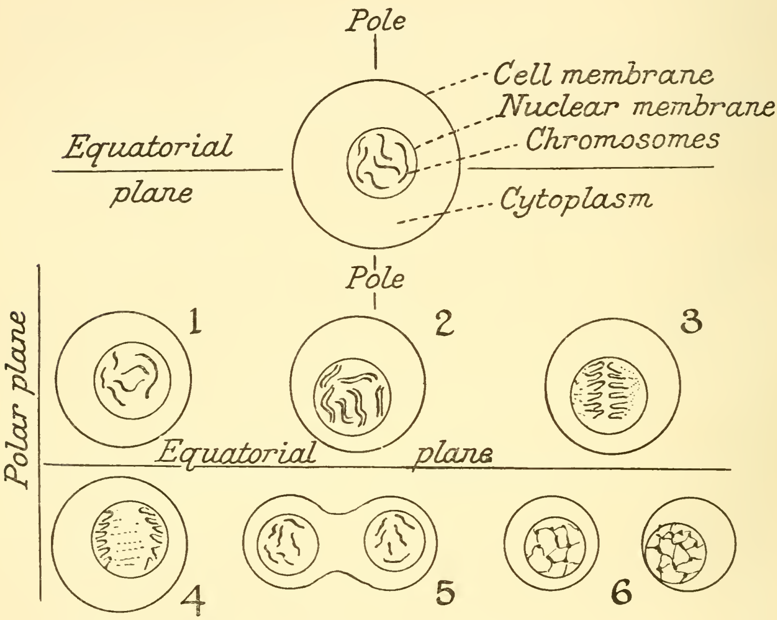


FIG. 22.—ESSENTIAL STRUCTURES IN A CELL ABOUT TO DIVIDE.

1–6, Places in the mitotic division of a cell.

cell peripheral to the nucleus is called *cytoplasm* and in the latter there are bodies (" mitochondria," " Golgi-bodies," " centrosomes," etc.) which do not concern us here. Within the nucleus the most significant substance is the *chromatin* (see Section 73*a*). In general the chromatin does not appear to have any very definite arrangement in the nucleus unless the cell is about to divide. Then it becomes assembled as a series of little rods, the *chromosomes*, and the number and general arrangements of these are very characteristic. In all the cells of the tissues of an animal or plant

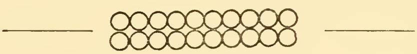
body the number of chromosomes is always the same and it is also the same for all individuals of the same morphological category. The number varies from 2 to about 150, but the most frequent values are about 40 to 60. The chromosomes are very small and can only be seen well under the highest magnifications of the microscope.

The appearances seen under the microscope when the cell divides are (typically) as follows (there are very many divergent details):

(1) The typical number of chromosomes form; (2) then each of them becomes double (by reason of its splitting lengthwise); (3) the two series of half-chromosomes become arranged as a "plate" in the equatorial region of the cell; (4) they are then drawn apart so that they come to lie towards the polar regions; (5) the nuclear membrane re-forms round each group of chromosomes so that the cell comes to contain two nuclei: at the same time it begins to suffer constriction round its equatorial region; (6) finally the constriction becomes deep and narrow and the cell divides into two daughter-cells each containing a nucleus.

The cells then differentiate to some extent and each of them usually grows to the size of the parent-cell.

Evidently the essential nature of this process is the exact division into two of all the significant parts of the cell. The chromosome is really a row ("linear series") of smaller units (the *chromomeres*), thus—  —and each of the units must be (halved for, by hypothesis, they are all different). So the chromosome must split lengthwise thus:



—plane of the "splitting."

It is believed that other essential bodies in the cytoplasm also divide, like the chromosomes do. Obviously the process mitosis ensures that every one of the essential things in a cell doubles itself so that when the parent-cell divides a complete "outfit" of parts goes into each daughter-cell. These outfits are then reassembled as complete nuclei and cytoplasmic apparatus and mass-growth occurs, when the daughter-cells assume all the parental form and characters. There must be a mechanism of mitosis, but we have no knowledge as to its nature.

II ANIMAL AND PLANT REPRODUCTION

When it reproduces an organism doubles itself and the characters, form and potencies of the original organism appear in each of the doublets. The " original " organism may be called the " parent " and the doublets may be called the " daughter-organisms." The daughters can be recognized as belonging to the same " category " as did the parent (see Section 77).

(This definition is of the nature of a " first approximation." It is amplified in the following sections.)

63. *ON REPRODUCTION IN UNICELLULAR ORGANISMS*

A unicellular organism (a *Protozoan* in the cases of the animals, or a *Protophyte* in the cases of the plants) is essentially a single organic cell. Typically it reproduces by division, as described in previous sections, and the division is probably one of mitosis in most cases. But it is generally impracticable to observe, with sufficient accuracy, the finer details in the very smallest organisms (such as bacteria) and no doubt the process is greatly modified with respect to the scheme in Section 62*a*. Thus the organism doubles itself and ceasing to exist as *one* organism (the " parent ") it simultaneously appears as *two* organisms (the " offspring "). The latter can be recognized as of the same kind as was the parent.

The process is adequate for continued reproduction *ad infinitum*. It is the only method by which Bacteria and Cyanophyaceæ reproduce. The giant Redwood trees are known to have lived 2,000 years and throughout that period they have grown—that is, their cells have reproduced by simple mitotic division. Fibrous connective tissue-cells are known to have existed in artificial culture and to have divided thousands of times. So also with some cultures of mice cancers kept in laboratories.

63*a*. Senescence and Rejuvenation in the Reproduction of Unicellular Organisms. Some Protozoa can be kept under laboratory conditions (that is, in small vessels or aquaria) and continuously observed. All the individuals in such a culture, or " strain," are known to have resulted from the division of one original organism. It has been observed that such a strain tends " to die out." The rate of reproduction by division gradually decreases until finally it ceases. Then the individuals of the

strain must be "rejuvenated" in order that reproduction may again begin. Rejuvenation may be effected by "conjugation" of pairs of the senescent individuals (see next section). But it can also be effected by the addition of some "stimulant" substance to the water in which the strain lives. In this way reproduction may be continued indefinitely—or senescence may be prevented from occurring.

But it is well known that wild animals may not reproduce when kept in artificial conditions, in captivity, and we may not, without some reservations, extend the results of laboratory observations to the cases of organisms living naturally "in the wild." And our knowledge of the indefinitely persistent reproduction, by simple division, in the cases of Bacteria, etc., indicate that "senescence" must not necessarily be associated with the reproduction of the unicellular organisms.

63*b*. Conjugation—the Transition to Sex. When senescence occurs in a strain the process of conjugation may occur.

Gross aspects of conjugation. Two similar individuals (for instance, two *Paramœcia*) approximate and their bodies partially coalesce. Then the individuals separate and each of them begins again to divide with full vigour. After a time senescence occurs and is again followed by conjugation and so on.

Finer aspects of conjugation. The process is variable in detail. In *Paramœcium* it occurs as follows: there are two "conjugants" and each contains two nuclei (macro- and micro-nuclei). When the conjugants coalesce (or before that, perhaps) one of these nuclei divides several times and two of the daughter nuclei that so arise have special significance—these are the stationary and migrant ones. In conjugation the stationary nucleus remains in its parent-organism, but the migrant one passes over into the body of the other conjugant and fuses with the stationary nucleus of the latter. Thus:

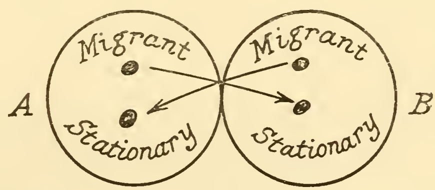


Fig. 23.—Diagram of the Essential Process in the Division of Paramœcium.

After this interchange of nuclei the conjugants separate and each resumes division with normal vigour.

63*c*. THE MEANINGS OF CONJUGATION. These are twofold :

i. Rejuvenation. Senescence is not understood. It is said to be due to (*a*) progressive increase of nucleoplasm ; (*b*) progressive increase of cytoplasm ; (*c*) decreased rate of metabolism ; (*d*) general lack of balanced activities that are not regulated. These statements mean little. We see, however, that with increase of specialized activities, senescence occurs. On the whole it is in the relatively undifferentiated organisms and cells that mitotic cell division tends to continue indefinitely (but see later in respect of vegetative reproduction). With this slackening of reproductive activity some stimulus to cell division appears to become essential and it is afforded either by some artificial food substance, or chemical change in the nutritive medium, or by conjugation—which brings some foreign substance, or something that sets up readjustment of some kind, into the senescent organism.

ii. The transition to sex. And certainly conjugation changes the " organization " of the organism. This organization is located in the nuclear constituents of the latter and when two organisms conjugate the nuclear constitution of each is changed. Not only is there a reproductive stimulus but some change in that which confers " characters " on the organism. In the higher organisms such changes in the developmental organization are certainly effected by sexual reproduction.

In typical conjugation the conjugants are the whole organisms and they are alike in characters. In other cases one of the conjugants is relatively large and passive, while the other is small and active. In typical sexual reproduction the conjugants (now called " gametes ") are usually markedly different : one (called the *ovum*) is large and passive and the other (called the spermatozoon) is small and actively motile. Thus in a typical conjugation among unicellular organisms typical sex is foreshadowed.

64. *ON REPRODUCTION IN MULTICELLULAR ORGANISMS*

The multicellular organism is also *multi-organismal.* Its (arbitrary) origin is a single cell, say the fertilized ovum. This reproduces by mitotic division and the result is a great number of originally similar cells which cohere into one assemblage. By

far the greater number of these cells differentiate into tissue-units—muscle-cells, bone-cells, nerve-cells, etc.—and they undergo tectonic arrangement into a body, or soma. But a relatively small number of the original cells remain in an undifferentiated condition and they are usually localized in some particular part of the body as *germ-cells.*

At about the time of reproductive activity the germ-cells reproduce by mitotic divisions. Consider such a fish as a plaice. In its body there are the gonads (ovaries in the female and testes in the male). Consider the ovaries (1 in Fig. 24). These organs are sacs and their walls are lined by germinal epithelium. The

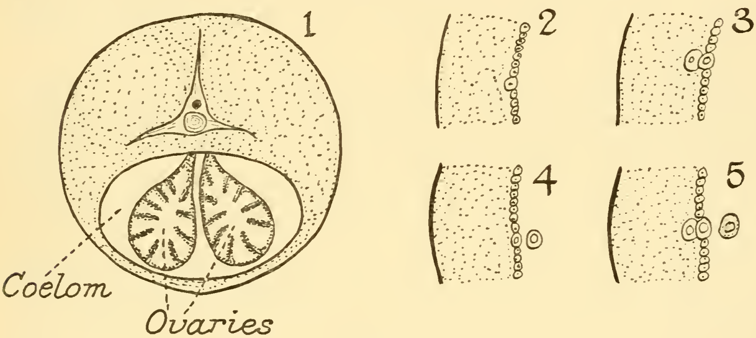


FIG. 24.

1, Transverse section through the body of a fish ; 2–5, stages in the proliferation of a small part of the germinal epithelium in the ovary.

cells of this epithelium are mostly germ-cells. Consider a small part of the germinal epithelium (2 in Fig. 24) :

Consider *one* germ-cell : it divides mitotically, 2, 3, and one of the daughter-cells is shed out into the cavity of the ovary, 4 ; the remaining cell still occupies the epithelium and it divides again, 5 ; one daughter-cell from this division passes out into the ovarian cavity and the other remains in the epithelium and so on. By and by the ovarian sacs become filled up with germ-cells (unripened ova). Presently these cells mature, imbibe water, swell out and become fully developed ova.

This is called a process of proliferation of the germinal epithelium. In innumerable ways the process is modified among animals. Ova or embryos are spawned, gestated, born, etc., but the essential thing is that the germ-cells proliferate.

In such a multiple reproduction as that of the plaice we say, about the fish, that "it" reproduces some hundreds of thousands of ova during its breeding season. But we should say, about the fish, that "they," that is, the germ-cells, reproduce.

For the germ-cells, every one of them, is a plaice. An animal is not simply an active, functioning thing: *it is a career* (see Section 69*c*) and the egg, embryo, larva and adolescent plaice are *phases* in the career. In all these phases there is identity of the organism: we could observe it continuously as a unitary thing throughout them all. The plaice-egg is certainly the species, *Pleuronectes platessa*: it is recognizable as such and no other kind of egg in the sea can be confused with it. The diagnostic characters of the egg are included in the definition of the specific category.

Similarly, we can observe the gonidial (germ) cell pass continuously into the matured egg so that it is identical with the latter in that gonidial cell and egg are phases in the continuous career of a unitary thing that preserves its identity throughout all its phases. The gonidial cell has all the potencies of a plaice-egg—and of no other kind of egg.

Therefore the gonidial cells are truly organisms that belong to a known category. Each such cell duplicates itself when proliferation of the germ-cells occurs and these doublings, that result from the mitotic divisions of the gonidial cells, are the essential acts of reproduction. Therefore the definition of Section 63 is valid for the multicellular organism. In the latter, considered as a sub-kingdom of life the simplicity of this conception is destroyed by sex. Innumerable modifications in the processes of reproduction occur. Nevertheless, the essential nature of the latter is such as we have indicated above.

65. *ON ASEXUAL REPRODUCTION IN THE MULTICELLULAR ORGANISMS*

In a great number of plant and animal organisms reproduction is essentially the proliferation of germ-cells. In many cases the latter, which are then called *spores*, *conidia*, etc., simply divide without conjugation or sex and the resulting cells undergo differentiation into tissue-units, and assembly into the bodily form.

Thus a germ-cell reproduced in a higher, multicellular plant, for instance, may develop at once, and without the stimulus of

conjugation or fertilization. The whole conditions of reproduction, in this mode, may, however, be greatly complicated by an alternation of asexual and sexual reproduction.

65*a*. Vegetative Reproduction. Simpler conditions than the above ones are characteristic of many of the higher plants. Such organisms may reproduce by "buds," "grafts," "cuttings," "slips," etc. Here the cells of the ordinary, somatic tissues can divide, differentiate and undergo tectonic assembly so that another plant which is of the same category as the parental one is reproduced from a small piece of the latter. The somatic cells, in such a case are not strictly differentiated from germ-cells and most cells in the fully developed organism must be regarded as reproductive ones.

Roses reproduce exclusively in this way (by apogamy). The plants do not bear seed. Willows, poplars, sugar-canes, some bananas, etc., reproduce by strictly asexual methods, and vegetatively.

65*b*. Budding in Animals. Similarly, some animals, the familiar *Hydra*, for instance, may simply bud. A protuberance forms on the outer parts of the body and this contains cells that have formed by the divisions of some cells from each germ-layer (see Section 70). The mass of cells forming the bud differentiate and are assembled into a new organism of the category of that one which formed the bud. Such cells are not germ-cells but are simply somatic cells. The potencies for development of these cells are, however, greater than are those which divided in the parental body so as to form them.

Again, there are innumerable modifications of the process of budding in animals. The essential thing, however, is that small "samples" of somatic cells can reproduce the whole body by their reproductions. In such cells, as they are placed in the parental body, there are qualities, or potencies, over and above those of ordinary bodily functioning.

66. *ON SEXUAL REPRODUCTION*

The essential condition of sex is that the germ-cells are of two kinds, "male" and "female." The male germ-cell, or *gamete*, is usually small and actively motile and it is called the *spermatozoon* in animal organisms. It is formed by the

division of a pre-existing gonidial cell in the male *gonad*, or testis, or essential male sex-gland. The female germ-cell, or gamete is usually large and inactive and it is called the ovum in animal organisms. It is formed in the ovary, or essential female sex-gland, by the division of a pre-existing gonidial cell.

The conditions in the higher plants are essentially similar—when we allow for the alternation of sexual and asexual generations. The male gamete (corresponding to the spermatozoon in animals) is the *antherozoid*, *pollen-nucleus*, etc. The female gamete (that corresponds to the animal ovum) is the *oosphere*, *egg-cell*, etc.

Thus two kinds of germ-cells, the gametes, are reproduced whereas, in the typical unicellular organism, there is only one kind of germ-cell and this is also the unicellular organism itself. In typically sexual animals there are clear indications that either the male or female gametes may, of themselves, develop into organisms. The ovum may do so in parthenogenetic animals (see Section 68) and in irregular fertilizations it may happen that the spermatozoon may, by itself, proceed to develop.

But what usually happens in sexual reproduction is that the ovum (or oosphere, in plants) is fertilized by the spermatozoon or antherozoid, or pollen-nucleus, in plants). There is conjugation of the gametes, just as there may be conjugation of unicellular organisms.

66*a*. Secondary Sexual Characters. In general animals are differentiated bodily into males and females. The essentials of maleness and femaleness are the existence of the male sex-glands, or testes, and of the female sex-glands, or ovaries, respectively. But there are also bodily differences.

External sexual organs. Typically there is *copulation* of male and female animals. This is analogous to the partial coalescence of *Paramœcia* (Section 63*b*). In copulation the gametes (ova and spermatozoa) are brought together and so there are generally receptive cavities (vagina, etc.) in the females while there are intromittent organs (the penis, etc.) in the males. In copulation the spermatozoa are placed in the receptive cavity, where they come into proximity with the ova.

But in some animals (some fishes) there may be no external genitalia whatever. Ova and spermatozoa are simply extruded from the bodies, or *spawned*, and they come into proximity in the water in which the animals live.

Accessory and unessential sexual characters. Certain characters of significance in mating may distinguish the sexes. Horns, antlers, differences of teeth, etc., are of this kind. Other sexual characters are hair on the face, or elsewhere, in males but not in females ; differences of size, colours, etc. There are innumerable modifications of this kind and the significances of many accessory and unessential sexual characters are obscure.

Nutritive organs. Finally the female animals are usually provided with organs for the carriage and nutrition of the embryos and young. Such organs are brood-pouches, egg-sacs, marsupial pouches, apparatus in connection with the egg-tubes, uteri, etc., the placenta yolk glands, etc. Such accessory, nutritive organs are very numerous and varied in forms.

66*b*. FERTILIZATION. The germ-cells conjugate in an analogous, or essentially similar way to the conjugation of two unicellular organisms.

For the moment we need not consider the processes by which the germ-cells *mature* (see Section 81). In all the gonidial cells there are the same number of chromosomes. (This is not strictly true, for there maybe reduplication of chromosomes, fragmentation of chromosomes, supernumerary chromosomes, "polyploidy," linkages of chromosomes, or even actually inconstancy.) Subsidiary hypotheses are devised to account for these deviations but, for simplicity in exposition, we assume that the number of chromosomes, in all the gonidial and somatic cells of all the individuals of a species, is quite constant.

In fertilization the gametes—say the ovum and spermatozoon—come into contact. The sperm-head, which is practically the "condensed" nucleus of the spermatozoon, penetrates the egg-membrane and comes to lie in the cytoplasm of the ovum. Hitherto the chromosomes have apparently been fused together in the sperm-head, but now they are resolved into discrete bodies.

At this stage, and as the result of maturation (Section 81) the number of chromosomes in the ovum-nucleus and the sperm-nucleus is exactly one-half of the number in a gonidial, or somatic cell. Say that there are 6, *A B C D E F* in the sperm-nucleus, and *a b c d e f* in the ovum-nucleus. What happens next varies considerably in different species, but we take what appears to be the typical and essential series of events.

The egg- and sperm-nuclei (the pronuclei) lie side by side in

the cytoplasm of the ovum (Fig. 25, 1). The chromosomes of these pronuclei may be separately visible, or their materials may be dispersed as a " reticulum." Next the separate pronuclei lose their sharpness by dissolution of their membranes. The

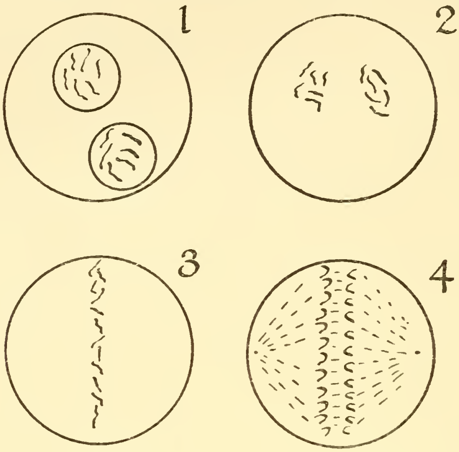


FIG. 25.—DIAGRAM OF THE PHASES IN A TYPICAL PROCESS OF FERTILIZATION OF AN OVUM.

chromosomes take on definite shape and come to lie near each other. Then they are arranged in a " plate " occupying the " equatorial " region of the fertilized ovum (Fig. 25, 2). Each chromosome splits lengthwise (Fig. 25, 4) and the half-chromosomes (24 now) lie in an approximate plane near the " equator " of the egg-cell. These half-chromosomes draw, or are drawn, apart towards each pole of the egg-cell. The egg-cell now divides into two daughter cells and further divisions occur as the ovum segments (Section 70*a*). Schematically the process is as follows :

Sperm nucleus		*Egg nucleus*		*Nucleus of fertilized ovum*
A		a		A
B		b		B
C		c		C
D	+	d	=	D
E		e		E
F		f		F
				a
				b
				c
				de
				f

The first segmentation division :

Splitting of the chromosomes		*The first two blastomeres*		
A A		A		AB
B B		B		CD
C C		aC		EF
D D	=	bDe	+	ab
E E		dEc		cd
F F		Ff		ef
a a				
b b				
c c				
d d				
e e				
f f				

The meaning of fertilization. Probably the most significant aspect of fertilization is the stimulus of the entrance of the sperm into the ovum. This " activates " the latter so that reproduction of the ovum-cell, by mitotic division, is set up. (Nevertheless, such activation is not absolutely necessary : see Sections 63–68*a*.) But equally important, perhaps, may be the addition to the ovum-nucleus of agencies carried by the sperm-nucleus : these agencies add male potencies to the female egg-cell.

66*c*. The Distribution and Determination of Sex. In most multicellular animals that reproduce sexually the number of male individuals is approximately equal to that of the females. When this is apparently not the case we may suspect that the life-histories of the males and females are so different that it may be difficult to " sample " the population in question and find the true ratio of males and females.

Dwarf and complementary males. Nevertheless, there are cases where the males are small, parasitic on the females, or otherwise so modified that the true ratios of the sexes may not easily be observed, or even may be greatly upset on development.

In general, in wild nature, the female is the larger and more active and longest-lived of the two sexes. The natural rates of growth, habits and longevity may differ. This again may upset the sex ratio.

The determination of sex. The approximate equality of the two sexes, and the fluctuations of the ratio, suggest that random causes are involved in the establishment of maleness and femaleness in an embryo. In multicellular organisms the condition of herma-

phroditism (see Section 67) is about as common as that of separate sexes. In practically all the plants this is the case and in all groups of higher animals hermaphroditism in individuals may occur. In most animals the male has rudimentary, or vestigial female characters and *vice versa*.

Mendelism and Sex. Sex can be regarded as an allelomorphic character (see Section 80). That is maleness and femaleness are mutually exclusive characters (but see hermaphroditism, "intersexes," "sex-mosaics," "gynandromorphs," etc.). A female animal may carry "recessive" maleness and *vice versa*. Sex may be "linked" with other characters (Section 80). There is evidence that of the spermatozoa produced by the individuals of a race, some may be male-determining and others female-determining. So also with the ova. These sex-conveying potencies are regarded as inherent in the chromosomes of the ova and spermatozoa and subject to reassortments at random (Section 80*d*). The hypotheses are rather complex and are mainly logical ones.

Nutrition and sex: sexual hormones. There is also evidence (even in human populations) that sex ratios may be affected by the nutrition of the eggs, or embryos, or pregnant mothers.

There is plenty of evidence that the sex glands provide substances which circulate in the blood and may affect the nature of the accessory, or unessential sex-characters. Castration, in either sex, in many animals, has marked effects on bodily characters (plumage, voice, etc.). There is even evidence that sex may be reversed. It has long been known that old hens may begin to "crow" as they cease to lay eggs. Even male sex glands may develop in such animals.

67. *ON HERMAPHRODITISM*

Most of the higher plants have *both* male and female sex organs. Most of the great groups of animals contain sub-groups that are hermaphrodite and this condition may be present in large and important groups of animals. Exceptionally hermaphroditism occurs in practically all animals—even in man.

In this condition, when it is typical, the same individual is both male and female—that is, has functional ovaries and testes. Functioning of both sex-glands may be simultaneous and copula-

tion may be reciprocal. Or an animal may alternate between the male and female conditions—only one sex-gland functioning at a certain period.

Structural (*and imperfect*) *hermaphroditism*. Both ovaries and testes may have developed in the same individual but only one or the other may function. Because of imperfect, or unregulated embryonic development the external genital organs may be abnormal so that a true female (carrying an ovary) may simulate a male and *vice versa*. In such cases (even in man) sex may be indeterminate from external indications. Or there may be " intersexes " where individuals recognizable as females may have male organs, and *vice versa*.

Plainly the animal organism, in general, is fundamentally both male and female and the condition in which the sexes are placed in separate individuals is a secondary one.

68. *ON PARTHENOGENESIS*

Parthenogenesis is virgin-reproduction. It occurs in several groups of animals and the condition is either facultative or obligatory: that is, the animals may, for a time, reproduce sexually and then, for a time, parthenogenetically (facultative). Or the only method of reproduction that is known may be parthenogenesis (obligatory). We must regard the animal so reproducing as a female, for its germ-cells have all the appearance of ova. They are simply emitted, or laid, by the parent and they develop without being " activated " by a spermatozoon, or in any other way that is apparent (see below). In the obligatory, parthenogenetic animals we may speak of all the individuals as females, in respect of the appearances and modes of origin of the germ-cells. There are no males. There may be said to be " sex " but not in the sense of our former definition of the term—which definition includes the appearance of two kinds of germ-cells, a particular mode of " activation " of the ovarian cell by the testicular one and the consequent processes of amphimixis.

68*a*. Artificial Parthenogenesis. Finally it is to be noted that there are animals which are typically differentiated into males and females but in which the female gametes, or ova, may be made to segment and develop without being fertilized, in the usual

way, by the penetration of a spermatozoon. The activation can be brought about in various ways, such as by the addition of minute quantities of inorganic salts to the fluid in which the ova are living. Typical development, as in a normal parthenogenetic animal, may thus be affected.

CHAPTER VI

DEVELOPMENT

By a developmental process is meant a series of changes in the course of which an organic system assumes a specific configuration. The systems may be (1) the little fleshy bud which forms at the place where the appendage of a crab has been broken off; (2) the "proud flesh" which forms in the scar of a wound that is about to heal and (3) ova, spermatozoa, buds, spores, etc. The corresponding specific configurations are (1) the regenerated limb of the crab; (2) the normal, vascular, muscle, nerve and connective tissues which are formed when the wound heals up; and (3) the organisms into which the ova, spermatozoa, spores, buds, etc., develop. In the following sections of this chapter we shall restrict the discussion to the cases of fertilized ova which develop into animal organisms, noting that the fundamental principles expounded can be made, with the necessary qualifications, to apply to all other ways in which animals reproduce.

69. *ON ANIMAL LIFE-HISTORIES*

A life-history begins when some cell in the gonad (or elsewhere) of the animal body divides so that a free gonidial cell is essentially detached from the parental body and undergoes the process of *maturation* (Section 81*a*). The matured, gonidial cell may be spawned, or emitted, from the body of the parent or it may come to be lodged in some cavity of the parental body (such as the uterus) but it is not then part of that body and it is only associated with the maternal body to the extent that it receives nutritive materials from the latter.

Development begins with the maturation of this gonidial cell. We consider the processes of maturation in the following chapters, noting merely in the present place that it involves meiotic cell divisions, in the course of which the nuclear materials of the gonidial cell become rearranged and either a matured ovum, or

spermatozoon, is formed. The ovum, or spermatozoon, must be regarded as an organism of the same kind as the parental organism from which it was detached. It has, in a way, all the characters of the parent, but those characters are potential in it. In development (and still restricting the discussion to the ovum) we see that these potentialities become realized so that, in the developmental process, the ovum passes through changes such that it gradually assumes all the specific characters of the parent.

Fertilization. In the majority of animal life-histories there is conjugation of an ovum with a spermatozoon before embryogeny begins, but this is not essential. The ovum, in many cases, can be made to undergo embryogeny without being fertilized by a spermatozoon and in the cases of parthenogenetic reproduction there is no conjugation. We shall not, therefore, consider here what is implied in the latter process. The changes of immediate interest to us begin when the ovum becomes activated.

69*a*. TYPES OF ANIMAL LIFE-HISTORIES. First we take those which are usually called *direct*. There is embryogeny such that the ovum develops within the body of the parent, as when the development proceeds within the uterus of the mother. Or there is embryogeny which is associated with an ovum that has much yolk in connection with it—this is the case with the eggs of birds, elasmobranch fishes, etc. The essential ovum, or " germ," is always a small body and as development proceeds it increases enormously in mass. It must, therefore, be supplied with nutritive material to allow of this increase. In many cases this material comes from the maternal blood, or other body fluids, *via* a placenta, or in some other manner. In other cases the nutritive material comes from the food-yolk, albumen, etc., which is associated with the ovum in the egg. Whenever, in such ways, the ovum receives immediate and abundant nutriment embryogeny proceeds continuously and usually rather slowly and after a period of " gestation " a young individual organism, having recognizably the specific characters of the parent, is born or hatched. Examples of such direct or continuous processes are seen in the life-histories of man and other mammals, in birds, in elasmobranch fishes, in squids and cuttle-fishes, etc.

Indirect, or discontinuous development occurs in the cases of ova that are " spawned " or emitted into the outer environment ;

which are small and are not provided with a large store of nutritive materials. The egg very often develops when floating freely in the sea, or other aquatic medium, or when lying on the sea bottom, etc. Development proceeds more rapidly than in the cases we have already mentioned, for the presence of food-yolk and other nutritive materials in the large-yolked egg impedes the process of segmentation of the ovum. But the development generally is arrested, or pauses, in the small-yolked eggs and what hatches from the egg-envelope, cocoon, etc., is not a creature with the morphological characters of the adult parent but a *larva*, which is usually very different in structure and habit from the parent. Very often the larva is an organism that is mobile, that can find its own food and is autonomous and freely living. It does not reproduce. For a time it lives independently of the parent. After this first larval phase, and when the organism has grown to some extent, development begins again in an accelerated manner. A " metamorphosis " is said to occur and the creature may rapidly take on the structure and habits of the parent so that it recognizably belongs to the same species as the latter. Or the metamorphosis may result in the appearance of another larval phase when the organism is still different in structure and habit from the parent and there may be three or four such larval phases in an indirect development. A good example is that of the common Barnacle which has the following life-history :

First phase. A creature called the " Nauplius " larva hatches out from the egg ;

Second phase. After living in the sea and growing the nauplius undergoes metamorphosis into the " Cypris " larva ;

Third phase. After a free life in the sea the Cypris metamorphoses into the adult form which then attaches itself to the sea bottom and rapidly changes into the Barnacle.

This is an example of a very great number of life-histories. Often, and particularly in the cases of animals which live parasitically in, or on the bodies of others the indirect, or discontinuous development may be a very complicated process. We need not go into details of such life-histories. From the point of view of the natural selection hypothesis their significance inheres in the opportunities for obtaining nutriment apart from the parent, or from the egg emitted by the latter ; for being widely distributed

throughout a much wider habitat than that frequented by the parent and for obtaining access to the host (if the organism is a parasitic one), etc. Very often the meaning of discontinuous development, on the selection point of view is, however, very obscure.

69*b*. THE FURTHER LIFE-HISTORY. When development has resulted in the appearance of an organism recognizably of the same kind as the parent there may be a further juvenile phase when parental care is still necessary to the well-being of the offspring. This is obviously the case with the human infant, the young of birds, etc. During the juvenile phase the young organism may be fed by the parent, protected, trained, etc. Even its bodily and mental development may still proceed. Even when the young animal may live and feed independently of the parent it is still reproductively immature. At some further phase there ensues the full development of the essential and external reproductive organs and the organism becomes able to emit ripe ova and spermatozoa and to copulate, if its reproductive mode is the sexual one. There follows then a more or less lengthy reproductive phase in which we see the complete animal. Certain sexual, bodily characters develop (hair on the face of the human male, for instance). Development may be regarded as leading up to this reproductive phase and when it comes to a pause the senescence of the animal may be regarded as leading away from the typical reproductive phase. In wild nature the animal usually dies catastrophically and it must be rare, in any case, when individual death happens solely as the result of " senile decay."

69*c*. THE SPECIFICITY OF DEVELOPMENTAL PHASES. We may summarize an indirect life-history, as for example, that of the Barnacle, as follows :

Ovum ⟶ Embryogeny ending in the *Nauplius Larva* ⟶ phase of pause ⟶ transformation to *Cypris larva* ⟶ pause ⟶ transformation to fixed, definitive phase, the adult *Balanus*.

And the history of a direct development, such as that of man, may be summarized :

Ovum ⟶ Embryogeny ending in the development of the *fœtus* which is born as the *infant* ⟶ juvenescent phase of continuous growth, with some differentiation, ending in the sexually mature individual at the age of puberty. It is customary to speak of embryonic, larval, post-larval, fœtal stages, or phases, and the

senses in which these terms are used will be understood from the above summaries. But these various phases are often not well separated from each other.

At all phases of the life-history the organism is a perfectly specific thing. If we have (from ordinary observation) sufficient knowledge of the life-histories of a group of animals the latter can always be identified as the separate species *at all stages in their life-histories.* Thus the eggs of British birds are all easily identifiable as species even when we do not know what the parent was. The eggs and larvæ of the British Teleostean fishes are all as clearly separable from each other and identifiable as are the fully-grown parents. Any life-history whatever is a specific career and is different from all others. The study of life-histories involves almost interminable detail and is the subject of the systematic works on Zoology—it is very incomplete and there are comparatively few animals of which we know the entire *curriculum vitæ.*

70. *ON EMBRYOGENY: I. THE GROSSER VISIBLE EVENTS*

Premising that we restrict the descriptions to such small-yolked eggs as those of the sea urchin, or the chordate, *Amphioxus*, the easily visible events of the embryogeny are: (1) The processes of segmentation, in the course of which the relatively large ovum divides by mitosis into a number of small cells. We may arbitrarily limit this process to the phase at which about 1,000 blastomeres, or formative cells, have been formed. (2) The process of formation of the germ-layers now begins. (3) From the germ-layers the organ-anlagen are formed and (4) there is then differentiation of the organ-rudiments so that definite tissues come into existence. For simplicity in exposition we describe embryogenesis in this way, but it must be noted, by way of qualification, that the phases (1) to (4) are rather arbitrary ones; that the cells formed in segmentation and later phases are not really separate units; that typical germ-layers are not always easily discriminated and that tissue-cells may be differentiated and again de-differentiated. But from the plain, schematic or typical descriptions we may all the more easily approach the essential problems of development.

70*a*. Segmentation. For convenience we regard the ovum

as spherical and we orientate it as we do a terrestrial globe. Actually the first division-plane of the segmenting ovum is usually determined by the place at which the sperm-head enters it in the act of fertilization. We shall say that this plane is "meridional," and that the second plane is also meridional and perpendicular to the first one. The third plane is again perpendicular to the former two planes, or is equatorial. Diagrammatically these division-planes may be represented as follows :

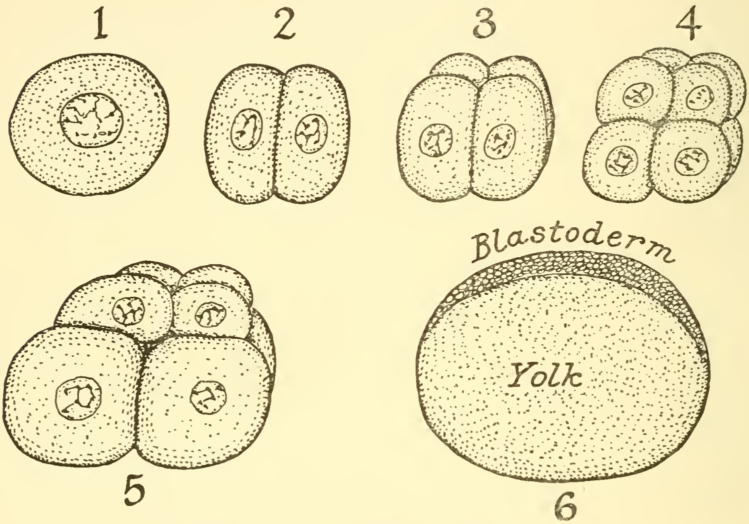


FIG. 26.—SEGMENTATION OF THE OVUM.

1, The undivided ovum ; 2, 2-blastomere stage, there is one meridional division-plane ; 3, the 4-blastomere stage, there are two meridional division-planes at right angles to each other ; 4, the 8-blastomere stage, there are two meridional division-planes (as in 3) and one equatorial division-plane at right angles to the two former ones ; 5, 8-blastomere stage in a yolky egg ; 6, the blastoderm in a large-yolked egg.

Close approximations to the above mode of segmentation occur very often and in widely different groups of animals and we regard it as the typical mode. (But the process may differ greatly from the scheme.) Usually the blastomeres are of nearly equal size up to this 8-cell stage, but after it there are, as a rule, two or more " tiers " of blastomeres—the " lower " and larger ones, and the " upper " or smaller ones. This is always so when the ovum contains much food-yolk (No. 5, Fig. 26).

In the extreme case, that of the large-yolked eggs of Teleostean

fishes, or birds, the process of segmentation may appear to differ greatly from that of the scheme of Fig. 26, 1 to 4 : Nevertheless, the typical mode is that of the scheme and the latter can be recognized, even in greatly distorted forms.

Typically, then, the process of segmentation continues until over 1,000 small blastomeres have been formed. These then become arranged in a particular way.

The Blastula. This is a little hollow ball, the wall of which is formed by a single layer of cells, which are often ciliated so that the embryo is mobile at this stage.

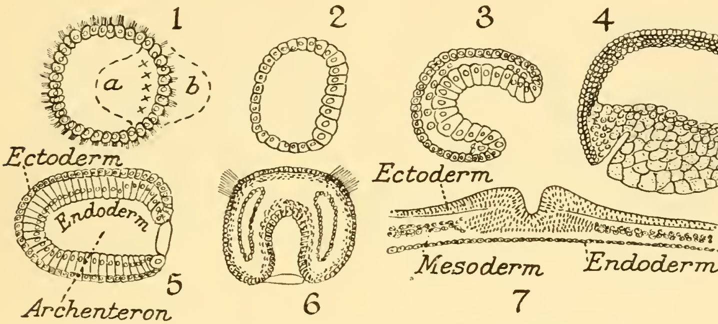


FIG. 27.—BLASTULAR AND GASTRULAR STAGES.

1, The blastula ; 2, blastula beginning to invaginate ; 3, invagination complete, the gastrula stage ; 4, gastrula in a yolky egg ; 5, complete gastrula ; 6, free-living gastrula larva of a worm ; 7, formation of the germ-layers in the hen's egg.

The process of gastrulation. At some part of the blastular wall, say at *x* in Fig. 27, 1, the cells divide more rapidly than elsewhere. The result must be that this part of the wall is either pushed outwards or inwards. Normally it is pushed inwards, so that the blastula is " dimpled." The process of " invagination " continues until a double-walled embryo is formed. This is the *gastrula* (Fig. 27, 3). The space between the two walls is the " segmentation " cavity and the inner cavity is the " archentron," which communicates with the outside by the development of the original dimple, or " blastopore."

Thus an embryogenic stage is attained which is called the " gastrula " and this occurs very often and in all the phyla of animals which have the three formative layers, endoderm, mesoderm and ectoderm. It may be difficult to recognize because

of the distortions introduced into segmentation by the presence of food-yolk in the egg (Fig. 27, 4). But it can very generally be recognized and we see in it a general, animal, developmental phase in embryogeny.

In the above figures the further development of the gastrula is represented in 6, a polychæte worm and in 7, the blastoderm, or formative membrane of the chick embryo.

The germ-layers. Thus are laid down three separate sheets of cells, or cell-layers—the *ectoderm* (or outer layer); the *endoderm* (or inner layer) and the *mesoderm* (or middle layer). There are cases of development in which these germ-layers are difficult to recognize: nevertheless, they are so often present in typical form, and they are easily recognizable in so many different kinds of animals that we may regard them as definitely tectonic arrangements of the cells of the embryo anticipatory of the further formations of the organ-anlagen. When they become established an important cavity appears in the embryo: this is the *cœlom* (see the above figure) and it is typically a cleft bounded by two layers of mesoderm, or it may be an irregular cavity, or one or more definite vesicles with mesodermic walls.

70*b*. The Potencies and Fates of the Germ-layers and Cavities. The germ-layers and cavities are the foundations of the subsequent tectonics in the development. In general these are the potencies of the various parts: we refer to normal and typical embryogenies, for there are many exceptions to the generalization.

Germ-layer or Cavity.	Organs and Parts derived therefrom.
Ectoderm . . .	Skin, sense-organs, brain, nervous system, etc.
Endoderm . .	Alimentary canal, digestive glands, skeleton, etc.
Mesoderm . .	Muscles, skeleton, connective tissues, circulatory system, renal organs, etc.
Archenteron . .	Cavity of the intestine, etc.
Cœlom . . .	Body cavity, pericardial cavity, cavities of renal organs, etc.

That is, by the divisions and subsequent cell-assemblies of the cells of each germ-layer the organs are formed, as in the above general scheme.

70*c*. ORGANOGENESIS. When the embryo has assumed the phase that is represented by the gastrula the process of formation of the organs *of the adult* phase begins. It must be remembered, however, that the gastrula itself is an organism and it may be (and very often is) a viable organism, mobile, irritable, and capable of independent existence in the wild state and carrying out all functional activities except those of reproduction. In the cases of embryos that undergo continuous development the gastrula (or the phase roughly corresponding to this) is, of course, dependent, for continued existence as a living thing, on the maternal nutritive substances, or on those that are included in the egg.

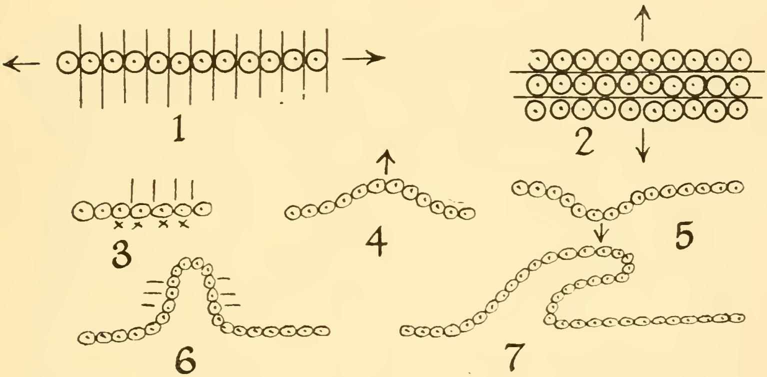


FIG. 28.—DIAGRAMS OF THE CELL-DIVISIONS IN DEVELOPING ORGANS.

The formation of the organ-anlagen proceeds by division of the germ-layer cells (we still refer to quite typical embryogenies, such as those of the chick). The process is that of cell-division, *the division-planes having strict tendency*. Complicated as the process may appear to be in such a description as that which follows it is apparently exceedingly simple and " natural " when one actually studies it in chick, or frog embryos that are observed from day to day throughout the period of organogeny.

Consider an epithelium, that is a sheet of cells, one layer thick. Let the division-planes be all parallel to each other and perpendicular to the surface of the epithelium (Fig. 28, 7), and obviously the sheet of epithelium will grow lengthwise, still remaining a sheet of one cell in thickness. Let the division-planes be all parallel to each other and parallel to the surface of the

epithelium (Fig. 28, 2), and obviously the sheet will increase in thickness but will not spread out lengthwise. Clearly the sheet will become warped, or curved, if the division-planes diverge from the parallelism.

Now suppose that only those cells in the region of the epithelium marked as follows, *x x x x*, divide by means of planes at right angles to the surface (Fig. 28, 3) ; plainly the surface will become arched, evaginated (4) or invaginated (5). Let the cell-divisions cease at the summit of the evagination but proceed at the sides of the latter (Fig. 28, 6), and it will easily be seen that the evagination

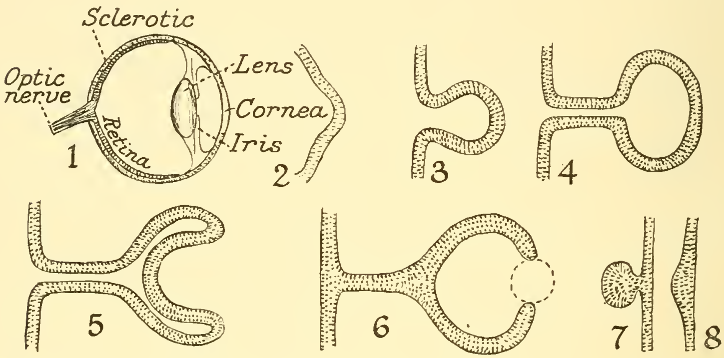


FIG. 29.—DIAGRAMS SHOWING THE DEVELOPMENT OF THE VERTEBRATE EYE.

1, the structural plan of the eye ; 2–8, stages in the development.

will continue to grow out from the epithelium as a tube (6), and if the divisions occur more rapidly on one side than on the other (as at 7) the tube will be bent over. In this way evaginations may take the forms of bent, twisted, branching, etc., tubes, bulbs, etc.

Now consider the mode of formation of such a very complex organ as the vertebrate eye : the structural plan of the latter is as indicated in Fig. 29.

The formative stages in such an organogeny are these : At (2) we see the epithelium of the fore-brain vesicle grow outward as an evagination towards the integument of the side of the head. This then becomes a bulb with a stalk (3) and the bulb enlarges, the stalk at the same time becoming attenuated (4). Thus the optic bulb is formed. The bulb then invaginates (5), becoming

double-walled, each wall being many cells in thickness. (Here we neglect the peculiar " choroidal " fissure.) At this phase the cells in the integument, just over the opening of the optic cup, thicken (8), form a little rounded body (7) which then becomes detached from the integumentary epithelium and comes to lie *in* the opening of the optic cup (at 6). This small, rounded body becomes the crystalline lens of the eye. Plainly we have now an optic anlage displaying all the structural plan of the vertebrate eye. In it all the cells are embryonic, or undifferentiated ones. It has come into existence by means of cell-divisions of an original, formative epithelium, which divisions have tendencies.

All organs are " blocked-out " in such ways—by cell-divisions that occur so that as the cells are formed they are marshalled into place in definite tectonic arrangements. The materials of these cells come from the nutritive substances at the disposal of the embryo. For simplicity we speak of cells as if they were separate bodies, but actually they remain in contact, or even in structural continuity with each other and their boundaries, or " walls," may even be obscure. They may be regarded as structural elements, or " building-stones " made on the spot as required. The description that we give of the formation of an organ-anlage does not, at all, " explain " that formative process : what has to be explained is the agency that divides the cells at the appropriate places and in the appropriate planes and *that* is the problem of development. But even the description is complex, though on practical acquaintance with an embryogenic process, it is very easy to follow.

71. *ON EMBRYOGENY : II. HISTOGENESIS*

When organogenesis has proceeded so far as the formation of the anlagen the cells are still embryonic, or undifferentiated in type. The eye, as a functioning organ, contains skeletal, connective, muscular, nervous, receptor, glandular cells, etc., but its anlage, as we have seen it develop, consists only of small rounded cells that are all similar to each other. As development proceeds these cells differentiate into categories and each category consists of cells that are tissue-elements. Thus there may be cartilage-cells, muscle-cells, the nervous cells that form the retina ; the nerve-fibres ; cells that make up blood-vessels ; the transparent

cells of the lens and cornea ; connective tissue cells ; pigment cells, etc. This is the process of histogenesis that continues that of organogenesis. It may be regarded as complete in the cases where development pauses and a viable larva results—as in the case, for instance, of the Nauplius larva of a Barnacle. When organogenesis is resumed, upon the transformation of the Nauplius into the Cypris-larva histogenesis is also resumed. In the cases of continuous development the histogenesis is seldom complete when the fœtus is born. Thus the differentiation of nervous tracts in the brain and spinal cord of the human infant is not completed until at least a year after birth.

The processes whereby embryonic cells become transformed into tissue-elements have been described in many cases of development. But obviously these descriptions are not necessarily explanations. How the cells in one part of an organ-anlage become muscle-cells while those in closely adjacent parts become, say, glandular cells is just as fundamental and unsolved a problem as that which is involved in the tectonic arrangement of the embryonic cells of the organ-anlage.

71*a*. DE-DIFFERENTIATION. As a very general rule both the processes of organogenesis and histogenesis are irreversible. But there are cases of development where the tectonics of the organs break down and the structure of the tissue-cells reverts to the embryonic, or undifferentiated type. This is the case with the Cirripede parasite, *Sacculina* : in the phase of the Cypris-larva the animal is completely developed and is able to lead an independent life in the sea (though it does not reproduce). When it attaches itself to its host (a crab) its organs and tissues lose their structure and the body apparently becomes a small mass of embryonic, or undifferentiated cells, which then enter into the body of the host. Somewhat similar phenomena are observed when the head of the Hydrozoon, *Tubularia*, is cut off and when a new head regenerates from the tissues of the stalk. First the cells of the latter part become de-differentiated and then a new process of organogeny and histogenesis begins. The same reversal of normal development may be seen in the growth of a malignant tumour, in, say a mammalian animal. The most striking thing in tumour growth is the very rapid divisions of the cells of the organ that takes on malignant characters, but more significant perhaps is the reversion to embryonic type, or

de-differentiation of the cells. In all these phenomena we see something very strange indeed—a suggestion, in a way, that the life-career of an organism from youth to old age may possibly be reversed.

71*b*. RE-DIFFERENTIATION. In cases like that of the parasite, *Sacculina*, there is a new process of differentiation. The embryonic cell mass that is injected into the body of the crab has no organ-anlagen or tissues. Presently, however, the process of organogenesis begins anew and is followed by histogenesis. But both the organs and the tissues of the adult, reproductively mature *Sacculina* that are so formed are quite different from those of the Cypris-larva that de-differentiated before infecting the crab. The process is very curious and is difficult to describe in terms of modern conceptions of genes (Section 74*b*).

72. *ON EMBRYOGENY: III. DISHARMONIES AND REGULATIONS*

For each organism there is a normal and specific developmental career and this may be remarkably constant and true to type: on the other hand, the development of an animal may display extraordinary departures from type. For instances: it would be easy to study very many thousands of flounder embryos incubating in a hatchery without finding a single abnormal specimen; on the other hand, malformations among the trout embryos seen in a fish hatchery are not infrequent. The ordinary experience of a medical man includes few cases of abnormal development: nevertheless, there are very numerous records of "monstrosities" of bizarre form. As in the cases of the trout embryos of abnormal type such human monstrosities are very seldom viable.

The reasons for abnormal development that introduces disharmonies into the embryonic structure are obscure. There are natural physical conditions: temperature, normality in the chemical state of the nutritive medium, etc., and these have certain optimal values for every development. In some cases the physical conditions, say, temperature, can be widely varied without doing more than retard or accelerate the rate of development—the result may be a perfectly normal embryo. In other cases relatively small chemical changes may be significant: thus the removal of the trace of calcium that sea-water contains may lead to the blastomeres of a sea-urchin embryo falling apart and living on as

separate cells. The addition of a little lithium salt to the water in which the same embryos develop may cause the archentron to be evaginated instead of invaginated.

The ovum may be fertilized by more than one spermatozoon —when notable abnormal embryos are developed. Doubtless the "heredity" of ovum and sperm may also lead to abnormalities —thus the occurrence of extra digits, etc., in a family. We consider such cases in later chapters. On the whole, just as with the general problem of development, there is no adequate theory of abnormalities, or disharmonies.

72*a*. Regulations of Development. Yet interference with the normal course of an embryogeny may not affect the formation of a normal larva. Some examples of such drastic interferences will be given and it will be seen that the embryo has a certain degree of power to compensate for these events and to affect regulations of embryogeny that lead to the normal result. There are limits to this power of regulation and these also we shall notice.

(1) The sea-urchin egg and embryo possesses power of regulation in a marked degree. A normal segmentation of the ovum results in an 8-cell embryo. At this stage the embryo is a "harmonious equi-potential system." If development be followed out it will be found that the eight blastomeres have certain fates, in that they are the precursors of different parts of the larva that normally forms: the various blastomeres develop in a certain, specific harmony. Nevertheless, these eight cells can be shaken apart from each other and then a regulation is effected. Each of them begins anew the process of embryogeny so that eight perfect but dwarf gastrula-larvæ come into existence. Therefore although each of the original cells of the segmented ovum has a "prospective value," which becomes realized in the normal development, it is also equipotential with all the other cells in that, if it should be necessary, it has also their prospective values.

(2) In the normal 8-cell stage (Fig. 26) the blastomeres have certain definite positions *relative to each other*. In the normal development what a blastomere is going to become depends on its position relative to the others. Thus in some embryos the cells on one side of a certain plane become the right-hand half of the body and *vice versa*. If now, the embryo at, say, the 4-cell stage be lightly compressed between two plates of glass

the cells, on further divisions, proceed, perforce, to arrange themselves as a plate, and not as a little hollow ball. Their relative positions are thus altered, so that if each cell had an inevitable fate an abnormal embryo would result. Nevertheless on release of the constraint the embryo effects a regulation so that normal development proceeds.

(3) In the sea-urchin development the blastula is a small, hollow ball the wall of which consists of about 1,000 cells arranged in a single layer. Here again the various regions of the embryo are normally destined to give rise to different larval parts. It is possible to cut the blastula in two hemispherical halves and, of course, it is entirely a matter of chance how the cut is made: obviously it may be made in very many different ways. Yet each half-blastula effects a regulation and proceeds to form a perfect, but dwarf gastrula.

In these examples any of the equipotential cells of the embryo behave as if what they are going to do depends on what the other cells are doing.

(4) When the frog egg has divided into two blastomeres it is possible to kill one of the latter by puncturing it with a hot needle. In such a case the other, uninjured, cell goes on developing *but forms a half-gastrula.* Apparently the power of regulation fails in such a case. But the half-gastrula may absorb the dead blastomere and then proceed to regenerate the missing embryonic part. And in other variants of the experiment the power of regulation can otherwise be shown.

72*b*. Isotropic and Anisotropic Ova. There are very many such experimental results and they are often apparently contradictory. But the contradictions largely clear up when we see that the process of development may have proceeded long before segmentation of the ovum begins. In many invertebrate eggs there are differently coloured parts, zones, crescents, etc., of the cytoplasm showing that the latter is already differentiated chemically: these we call anisotropic ova and we note that when segmentation begins the different parts of the cytoplasm become located in different blastomeres. This differentiation imposes limitations on the embryogeny and it happens that mutilation of such a segmented, anisotropic egg leads to the development of a defective embryo.

There will be a stage in the development of such an ovum

when the differentiation of the cytoplasm had not occurred and the egg is then isotropic, or of equal cytoplasmic constitution in all parts. This is the state of the sea-urchin ovum, and also of the 8-, 16- cell, and blastular larvæ. There is, as yet, no differentiation of the parts and the latter are still equipotential so that they can effect regulations. Some time, however, in the development this equipotentiality of the parts is lost.

Clearly the gonidial cell, before it matures, the matured and ripening ovum and the embryo in process of developing are phases in a life-history and at any such phase the thing that is developing is an organism. It takes up nutritive materials from its environment, chemically transforms these and assimilates them so as to form new cells. It assembles these cells as they come into existence in specific configurations that are the anlagen, or rudiments of organs, and it proceeds doing this, more or less rapidly perhaps, in spite of quite notable changes in the physical conditions of the development. If these conditions are violently changed the course of organogeny, or of the subsequent larval metamorphoses may be changed, but very often the embryo, of itself, can regulate its activities so that the normal development is effected. If the environmental changes are too violent a malformed embryo, or larva is, of course, formed. The developing organism may inhabit a highly specialized environment—as when it is *in utero* and is nourished by the maternal blood, or when it is part of an egg containing all the nutritive materials necessary for development, but these conditions are no more specialized than are those in which many adult, parasitic organisms live. On the other hand the ova, embryos and larvæ of molluscs, worms and hosts of invertebrate animals live in the open sea, obtain their nutriment from the substances in solution therein and behave in all ways as if they were independent organisms—except that their development is incomplete.

We now proceed to discuss the nature of the developmental process and first it is necessary to examine into the problems presented by the cell nucleus.

73. *ON THE CELL NUCLEUS IN DEVELOPMENT*

Typically the cell is a minute rounded body containing a nucleus. Apart from the latter the cell-substance or cytoplasm,

is a complex mixture of proteins, carbohydrates, lipoids, mineral salts, water, etc. We speak of an organ, tissue, embryo, etc., as a complex of cells—this is often justified and it is always convenient in exposition. But the cells are always in contact, or are structurally continuous with each other and often the boundaries between them are obscure, while infrequently we cannot speak of cell boundaries at all. When we can speak of typically bounded cells we recognize in them a very complex morphology: this is obvious when we remember that a " cell " may be any kind of tissue element, such as a nerve-ganglion cell, a muscle-cell, etc., or it may be an organism that is perfectly competent to carry out all the functions of a living thing—or it may be an ovum, when it has the potentialities of a complex multicellular, higher animal, but in this case its " morphology " is, in some way, latent in it and not accessible to minute anatomical study.

The cell-nucleus, or energid is always a constituent of a cell, or of an organic plasmodium without cell boundaries. It is always a distinctly bounded body, typically spherical in form. The boundary is the nuclear membrane and much of the contents of this may be regarded as proteins, carbohydrates, lipoids, phosphatides, etc. Characteristic of the nucleus, however, is the substance called *Chromatin* that it contains. Chromatin is usually recognized by the way in which it stains with a class of dye-stuffs—this is the origin of the term. Usually the chromatin is dispersed through the nuclear body as minute granules, or discontinuous filaments, or as small rounded bodies called nucleoli. Sometimes, as when the cell is going to divide, the chromatin assumes a definite morphology which is characteristic of the kind of cell. It then becomes segregated into a complex " skein," or a system of filaments, and typically it becomes broken up into a number of bodies called *chromosomes*. These are (typically) short rods, but they are also described as granules, of many different forms. There may be from two to nearly 200 chromosomes in a cell which is in process of division. Typically the number of chromosomes in such a cell is constant for the species of organism that is the cell, or which is a body composed of the cells in question (but the number is often not really constant.)

The chromosomes are minute bodies that are not far from the limits of visibility, as seen under a high-power microscope.

Typically they are single or double rods that may appear to be made up of single or double rows of granules, and such a structure is assumed even when it cannot always be observed. When we trace a cell throughout a series of activities the chromosomes may appear to lose their identity, ceasing to " take the stain " (and thus ceasing to be the chemical individual called chromatin). But since the typical numbers and approximate shapes of the chromosomes may reappear in further phases of the activity of the cell it has been customary to assume their continued existence, even though their substance appears to undergo chemical decomposition. Thus a certain morphology, additional to that which can really be observed, is assumed of the chromosomes.

We return to these matters in later chapters and it is important now to treat of

73*a*. THE CHEMISTRY OF " CHROMATIN." Chemical tests cannot yet be applied to the chromatin of a single cell, but some animal tissues such as the ripe testis of a fish, or the thymus gland of a mammal, are made up of very small cells with relatively large nuclei. In mass, then, these tissues consist predominantly of chromatin and the latter substance can be isolated from a large quantity of the tissue and so can be examined in a nearly pure condition.

Chemically, " chromatin " is *nuclein*, which itself is a salt of *nucleic acid*. What the cytologists see when they examine " chromatin " is the nucleic acid combined with some basic substance which is used as a " fixative." In the natural state, in the nucleus, the nucleic acid is combined with the (or a) protein called *protamine*. Protamine is one of the simplest of proteins and it is known to be composed of a chain of *tripeptides*, thus :

$$\text{etc.}—\left\{\begin{array}{l}\text{arginine}\\ \text{valine}\\ \text{arginine}\end{array}\right\}——\left\{\begin{array}{l}\text{arginine}\\ \text{serine}\\ \text{arginine}\end{array}\right\}——\left\{\begin{array}{l}\text{arginine}\\ \text{proline}\\ \text{arginine}\end{array}\right\}—\text{etc.}$$

These groups within the brackets are tripeptides and there may be about half a dozen of them in the molecule of a protamine. The substances, arginine, etc., are amino-acids and arginine is,

$$\begin{array}{ccccccccccccccc} & & NH & & H & & & & & & NH_2 & & & & \\ & & \| & & | & & & & & & | & & & & \\ NH_2 & - & C & - & N & - & CH_2 & - & CH_2 & - & CH_2 & - & C & - & C - OH. \\ & & & & & & & & & & & & | & & \| \\ & & & & & & & & & & & & H & & O \end{array}$$

The others are also rather simple in the chemical sense and so the substance called a protamine is, relatively to many other proteins (such as the globulins, hæmoglobin, the albumens, etc.), *a very simple substance.*

The nucleic acid can be separated from its protamine base. It is chemically complex but far less so than most of the substances of the animal body. Its chemical composition has been found to be as follows :—

Phosphoric acid — a sugar — guanine
|
phosphoric acid — a sugar — thymine
|
a sugar — cytosine
|
phosphoric acid — a sugar — adenine
|
phosphoric acid

(Thymus nucleic acid).

We can simplify this by imagining it to be made up of the four *nucleotides*. Each nucleotide consists of the three groupings of atoms :

|
phosphoric acid — a hexose carbohydrate — a purine base.
|

There are various nucleins and the main differences between them are in the kinds of carbohydrates and purines (or nitrogenous bases) that they contain. The structure of a nucleotide is, chemically, very suggestive :

(1) The phosphoric-acid groups are annectant substances, linking, releasing and re-linking the other groups ;

(2) The carbohydrates are in such states that they may be highly reactive, being stable when linked on to the nitrogenous bases, but oxidizing at once when set free.

(3) The purines, or nitrogenous bases are the simplest organic groups carrying reactive carbon and nitrogen.

The key substance of these nitrogenous bases is *urea*, which may be represented as

$$O = C\genfrac{}{}{0pt}{}{\diagup NH_2,}{\diagdown NH_2}$$

but the chemical reactions of which do not altogether support this formula.

It is the simplest possible chemical body which has all the characteristic organic elements, C, N, H, O. It is a body of profound metabolic importance ; curiously versatile in its chemical behaviour ; now readily undergoing disintegrations and again undergoing synthesis. It is obviously of the highest possible significance in the processes of animal metabolism. Now in the bases that make up the nucleotides, that is, in thymine, guanine, adenine, cytosine, uracil, etc., there are the purine and pyrimidine nuclei, or chemical foundations. These are all to be derived from the urea-skeleton $= C\Big\langle\begin{matrix}N =\\ N =\end{matrix}$.

It is difficult to consider this very peculiar chemical structure of nuclein without coming to the conclusion that it is, so to speak, the armament of rapid metabolic changes in the nucleus and its immediate cytoplasmic environment. The protamine part of the chromatin is probably chemically inactive : it is a stable substance, strongly basic, not digested by pepsin but broken down by trypsin. The nucleic acid, on the other hand, is easily disintegrated. Nucleases, or enzymes peculiar to nuclear structures, easily break it down. The carbohydrates in the molecule are very reactive when broken off from the nitrogenous bases. They may be oxidized, when much available energy is set free, or they may even afford oxygen to other systems. (Note, in this connection, the anærobic respiration of some cells by the disintegration of sugars.) The nitrogenous bases, when they are thus broken away from the nuclein molecule give the necessary materials for other syntheses. What we see in the nucleus is, for one part, obviously the means for rapid and versatile chemical reactions *on the minute scale.* Possibly the segregations of strongly reactive substances in multitudes of minute " vessels," the nuclei, in close proximity to each other yet always quite separable, is a condition of some significance.

We shall return to this matter of the chemistry of the cell nucleus in a later chapter. We have now to consider what is the nature of the developmental process.

74. *ON THE NATURE OF THE DEVELOPMENTAL PROCESS*

Any discussion of this matter is necessarily very largely historical—there is, at present, no working hypothesis of development and, at the most, we can only speculate, with very obvious limitations. The oldest, and still the prevailing conception is one that contains the idea of *involution*. An ovum, seed, bud, etc., does not appear to be the organism which it will become in the course of its development: nevertheless there is in it, somehow or other, that which will *evolve*, unfold, or develop into a particular kind of organism. This was the notion of development commonly held up to the time when the morphological method (because of the invention of the microscope) was applied to the study of embryology. When, however, it could easily be seen that there was nothing in, say, the blastoderm of the developing chick, in the least resembling the organs of the fowl the notion of involution was, for a time, abandoned in favour of that of *epigenesis*. From the relatively structureless blastoderm came the complex system of parts of the embryo: these *grew up upon* the blastoderm, apparently because of the action of the environmental agencies. But obviously the conception could not be maintained because it was easy to see that *different* blastoderms, exposed to *the same* external agencies gave rise to different kinds of organisms. It was necessary to postulate " internal factors " as well as external ones in a developmental process, and by and by these internal factors were apparently found when the complex architecture of the " germ-plasm " was revealed by the perfection of the compound microscope. So notions of involution, based on the morphology of the nucleus, were again applied to the investigation of development and such is the prevalent outlook at the present time.

The notion of " representative particles." This is very old, but it assumed modern form in the hypothesis of *pangenesis* elaborated by Charles Darwin. From all parts of the body of the organism particles were given off which had, in some way, the potentialities of the organs, or parts, from which they were derived. These representative particles became lodged in the cells of the gonads—the ova and spermatozoa—and when the embryogeny began the potentialities of the particles became realized in the organ-anlagen and tissues. The notion amplified the older one of

preformation, according to which the adult parts actually existed, somehow, in the ovum or spermatozoon. The cruder, preformationist notions sometimes expressed it rather naïvely, as, for example, when the human spermatozoon was actually figured as containing a homunculus. The well-developed preformist notions, as for example, that formulated in Darwin's pangenesis, were, of course, much more subtle, though they were incapable of experimental verification. So were the later preformation hypotheses of Weismann, and in our own time those of Morgan and his colleagues and pupils. There did seem, however, to be an actual basis of observational data in Weismann's speculations and so also with the later work which resulted from the partially abandoned Weismannism. Then came the " Mendelian Renaissance " and the methods of modern genetics and, when it became possible to make correlations between the results of breeding experiments and morphological changes in the constituents of the nuclei of the conjugating ova and spermatozoa, the modern preformationism did seem to have both observational and experimental basis. These latter notions of developmental processes we must now discuss.

74*a*. THE MORPHOLOGY OF THE NUCLEUS IN DEVELOPMENT. Certain things made it probable that nuclear processes are actually bound up with embryogenies and subsequent developmental processes. (1) The complexities of chromatin-structure opened out a new field for the application of the morphological method on the microscopic scale ; (2) the behaviour of the chromosomes both in the phenomena of maturation and fertilization were very suggestive of the significance of these nuclear structures. Such investigations led to the conceptions of *Weismannism*.

There appeared to be specific " outfits " of discrete chromosomes in all organisms that were minutely studied. Every cell in the *Soma* in all the individuals of a species of organisms has (*when it divides*) a certain number, N, of chromosomes, and every one of the *matured* ova and spermatozoa of the same individuals has (*when it is formed*) a number, half N, of chromosomes. The reduction of N to half N occurs in the processes of maturation. The numbers N and half N are not actually constant, as will be seen by a candid study of the results of individual investigations : still there is much in the general statement given above that

arrests one's attention. And, accepting this general result, we find that the exceptions to it can be explained by logical hypotheses.

In Weismann's time it was shown that the nucleus had a certain architecture and this was amplified—far beyond the observational bases. It was seen, occasionally, that each chromosome could be decomposed into discrete granules and these, or more minute parts that were not actually seen, were called *ids*—each *id* being regarded as *involving* all the characters of a complete organism. The ids were regarded as being made up of (ultramicroscopic) parts—the *Determinants*, each Determinant *involving* all the characters of an organ, tissue, part, or character. The Determinants were supposed to be made up of *Biophores* which were regarded as the ultimate living, material particles, corresponding, in a kind of way, to molecules.

The materials of which the cell-chromatins were composed, were the *germ-plasm*. This, if not an absolutely stable substance, was very nearly so and hypotheses were devised to account for changes in the natures of the germ-plasmatic elements, or determinants. But novelties in the history of a race of organisms —or what is called *transformism*—were regarded as due, not so much to changes in the determinants as to reassortments of the latter occurring in every act of sexual conjugation. In itself, as a complex system of chemical substances the germ-plasm was so nearly stable that it was unaffected by the environmental changes to which the *soma* or body was exposed. But whatever qualities the germ-plasm had were due to its chemical constitution.

Weismannism included a logical hypothesis of development. The chromosomes were regarded as linear arrangements of determinants and in an ordinary cell-division it was seen that the nucleus divided in such a way that all its visible parts were halved between the two daughter-cells. Thus let us suppose that a nucleus contains the determinants, a, b, c, d, e, f: when it is about to divide each determinant is halved thus $\begin{matrix} a & b & c & d & e & f \\ a, & b, & c, & d, & e, & f \end{matrix}$. One set of all the halves then goes into one daughter-cell and the remaining set into the other daughter-cell. Clearly, then, the daughter-cells are similar to the mother cell. Now apart from the peculiar meiotic nuclear divisions in the maturation of the gonidial, or germ cells, *all the cell-divisions in the course of the*

development of the fertilized ovum are of this equational kind and, so far as the chromatic material of the nucleus is concerned, there is no difference between them.

So Weismann postulated another kind of nuclear division. Let us suppose that the fertilized ovum contains the determinants, *a*, *b*, *c*, *d*, *e*, *f*. When it divides these determinants are supposed to become separated from each other during the nuclear divisions so that while the original cell (say the ovum) contained determinants of all the characters, *a*, *b*, *c*, *d*, *e*, and *f*, the daughter-cells would, each of them, contain only one determinant and would be instrumental in the development of only one organ, tissue, character, etc. Some time, then, during the segmentation of the ovum the various determinants would be sorted out and the embryo would become a mosaic of formative agencies, each of these being located in a single cell, or in a small number of such. These formative cells would then divide to form the organ-anlagen in virtue of the determinants carried by them.

This notion of determinants of structure was one of the essential parts of Weismann's hypothesis of development and it is both curious and instructive that it should have been accepted in spite of the want of any evidence that the segmentation cell nuclei differed from each other. Another essential feature was the notion that the formative agencies, or determinants, were physical-chemical in their nature—this we shall consider later. Now these two essential ideas: that of formative, particular agencies in the chromatic material of the nuclei, and that of the physical-chemical nature of the formative and particular agencies are also included in current, genetical hypotheses.

74*b*. "Morganism": the Genes. These current hypotheses hold that the chromosomes are linear series of discrete, chromatin-particles that *are*, or carry the formative agencies for, the development of certain organic characters. During the processes of maturation and fertilization these particles become separated, joined, sorted and reassorted and it is held that there is a correlation between the joinings, disjoinings, assortments, etc., of the formative particles and certain groups of bodily characters that develop in the organisms in which the joinings, disjoinings, etc., occur. It is true that the nuclear phenomena mentioned are not held to occur in the cell-divisions that occur after the fertilization of the ovum: nevertheless, it will be seen that the hypotheses

of Morganism are essentially similar, in some important respects, to those of Weismannism and, of course, that was their inspiration. We must regard Morgan's genes as expressing the same essential idea as the determinants of Weismann. Like the latter, they are located in the chromosomes although they are too minute to be visible. Cruder views regard them as physical-chemical in nature though the less naïve writers refer to them as the " carriers of hereditary qualities." It is said that something like rows of genes may be seen in the nuclei of cells undergoing maturation and there are appearances, in these changes, that suggest the joinings, disjoinings, reassortments, etc., of the genes. This is true, but it must be noted that different interpretations of the appearances have been made and that there is not general agreement among cytologists as to what actually occurs in the maturing germ-cells.

And it is expressly stated by Morgan that his hypothesis is not one of development, mainly because the processes of organogeny and histogenesis are not accompanied by any nuclear phenomena that can be associated with differentiation. Nevertheless, modern genetics does maintain that there is a correlation between phenomena that include joinings, assortments, etc., of the genes and the appearances in later individual life-histories of morphological characters and, to that extent, Morganism must be a hypothesis of development.

And it is to be noted that it is a morphological hypothesis and that, in some quarters, it is held to be the line along which (as in the past) the study of transformism and, therefore, the study of the evolutionary career must proceed. It implies little of what we may strictly call experimental investigation, though that is beginning and may be expected soon to reconstruct the hypothesis. In the sections that follow we shall further examine into its bases.

75. *ON THE DEVELOPMENTAL ORGANIZATION*

By this term we mean that which is involved in the development of the differentiated adult organism from the relatively undifferentiated ovum, spore, bud, etc. We shall endeavour to state with as little resort to hypothesis as possible, what the developmental organization appears to be.

i. It is not a material substance.

Weismannian determinants and, according to the cruder views, the genes of Morgan have been regarded as elementary constituents of the chromatin of the nucleus of the ovum about to develop. This substance, a nucleo-protein is supposed to undergo chemical and physical changes, *of itself and in virtue of its chemical and physical nature and quite apart from any other agency* so that the embryo comes into existence. The nucleo-protein must, therefore, (*a*) be able to select materials from the environment and chemically transform these into materials similar to itself ; (*b*) grow and reproduce by dividing itself and then the cell containing it, growing again and then again dividing and so on ; (*c*) orientate the angles of the division-planes, and divide more rapidly at some places than at others so that an assemblage of cells of definite, specific form comes into existence.

The physical analogy with these processes is crystal-growth. But the crystal-groups, such as the ice-flowers on a window-pane, " crystal-trees," etc., are *random* assemblages of crystals, all of which are of the same chemical individuality and geometrical form, whereas the assemblage of cells that is the fully-developed product of the hypothetical developmental material contains substances that are chemically different, and are chemically more complex than nucleo-protein. Further, this assemblage has a perfectly *specific* form. Again the constituents of the ovum, embryo and developed organism are colloids and not crystalloids. It will be clear, then, that candid examination of the processes of crystal-growth does not bear out the analogy. There are no chemical or physical processes that suggest how a physical-chemical system, *of itself*, can so react with its environment so that the processes, (*a*), (*b*), and (*c*) above, occur.

It is very curious that the view that the developmental agencies are material substances should have been held in spite of the elaboration of modern thermodynamical theory. Consider a physical-chemical system (such as nucleo-protein). If it undergoes chemical change (decomposes, hydrolyzes, oxidizes, etc.) of itself it does so only when energy is dissipated in so doing. This means that such " spontaneous " changes lead to energy-dissipation, to the decomposition of the substance into other substances which are chemically simpler, to chemical, statical equilibrium and to entropy-increase. After such reactions have occurred the

system has become stable and will no longer undergo change. Now a developing ovum, with the substances in its environment, is a chemical-physical system which undergoes changes. But in these changes the substances of the system become chemically more complex, the equilibrium is chemical-dynamic, and the entropy of the system decreases locally. Clearly the chemical and physical changes that occur during a development are not such as those that a complex chemical substance would undergo *of itself*: they are not " spontaneous " changes.

There are chemical-physical transformations that are *coupled* ones and examples are the photosynthesis of carbohydrate in the cells of a green plant, or in the apparatus and materials assembled by an experimental chemist. Here the dissipating energy of solar or other light is brought into association with the system, CO_2 and OH_2. Of themselves the latter compounds would not combine and of itself the energy of the radiation would dissipate. But in the natural events and in the experiment the molecules of CO_2 and OH_2 become energized by the radiation and their internal energy is greatly increased. These energized molecules then "spontaneously " dissipate their energy and this (as always) becomes the occasion for a chemical reaction, which is that of the combination of CO_2 and OH_2 (in the highly energized state) to form carbohydrate. The internal energy of the latter compound is less than that of the energized CO_2 and OH_2 (and that is " Why " it was formed), but it is greater than that of the unenergized CO_2 and OH_2.

And, therefore, the chemical and physical events of a developing organic system are to be compared with the events that occur in a system of coupled energy-transformations. Clearly there is an agency which effects the couplings and it is this that is the developmental organization.

It is true that a chemical-physical may *of itself* and with very great improbability, so change that its chemical structure may become more complex, its internal energy may increase and its entropy may decrease. The probability that this may happen is of the order of that of such an event as follows : all the bricks, mortar and other materials necessary for the construction of a small house might be thrown on to the ground *at random* and might still fall together, at random, into the form of the house. We have never heard of such an occurrence, so very improbable

is it, but organic developments are vastly more probable and so they suggest processes that do not occur at random, but which are tendential ones.

Lastly, we again look at the chemistry of chromatin, the hypothetical developmental substance. We note its relative simplicity ; the entire want of any suggestion, or indication of its power of self-differentiation. We note that all that chemistry suggests is that nucleo-proteid appears to be a material very suitable for rapid and versatile chemical transformations in conditions where these transformations may be directed ones. We notice, also, that there is no continuity of the chromatic materials in, say, the history of the maturation of a gonidial cell, or in the phases of the nuclear divisions that occur when the ovum segments. There are "resting phases" in which the nucleo-protein of the chromosomes is dispersed, hydrolyzed or otherwise chemically changes. It is true that the chromosomes are *reconstituted*, in their typical numbers and forms, after the resting phases. It is said that even when the chromosomes have lost their staining reactions—that is, *are no longer nucleo-protein*, "ghosts" of their forms may still be seen in the nucleus. But plainly this means that it is the morphology of the nucleus, and not its chemistry that we are studying.

ii. It is organismal in nature.

That is, whatever activities we see in the living organism are also in the developing embryo : the latter is mobile, irritable, assimilatory, etc., and it even reproduces in that it undergoes nuclear and cell-divisions. An algal zoospore or a polychæte trochospere larva are clearly autonomous organisms that move about and assimilate in sea-water. The embryo contained in a yolked egg, or developing in a uterus assimilates and grows in mass (although its most salient activity is the tectonic one and this overshadows the other activities). The developmental phase that we call a larval one is plainly a phase in which the thing that develops by metamorphosis is, in all respects save reproduction, an organism. We tend, somehow, to think of the developing thing as not yet, but about to become an organism, but this view is clearly inaccurate.

iii. It exhibits, in a predominant way, tectonic activities.

Although the thing that develops is truly an organism what is significant in its organization is a tectonic activity. It selects

materials from the physical environment, or from reserves in the egg, or from the blood-stream of the parent, and it assimilates these materials into itself as the substance of new nucleo-protein and cytoplasmic materials. But as these new cells are formed they are *assembled*, by definite, specific cell-division planes and rates of cell-divisions into specific cell-configurations so that organ-anlagen, and later on, tissue-configurations, are established. It is this assembling, building, or tectonic activity that is the one to which we mainly attend in a developmental process.

iv. The developmental organization is a specific complex of potentialities.

The fully developed organism which the ovum becomes has parts—body and limbs, alimentary canal, etc., but these parts are not, *as such*, in the structure of the ovum. In the terminology of the current geneticist hypotheses we say that there are " genes " in the ovum which by interaction with each other, with the cytoplasmic and external environmental materials and energies give rise to the parts. But we cannot see, or otherwise know about the genes (which, in cruder views, are regarded as ultra-microscopic in size.) Plainly the ovum has the power, or potentiality of *becoming* these parts when it interacts with its environmental materials and energies. Of course, it becomes one whole, unitary thing—the fully developed organism, but since different kinds of organisms differ from each other in respect of one or more characters, or parts, it is convenient to think about the potentiality of the ovum as multiple, though it is sounder to think about it as unitary. Thus we may, in exposition, speak about the organization as a complex.

And it is a specific complex in that it becomes an example of a particular kind, or species, or race, etc., of organism. This specificity of potentiality is in the organization and not in the environment with which it interacts : thus cod and whiting eggs develop in the same sea-water but one becomes a cod and another a whiting. The environment conditions and limits the process of development so that if these " external factors " are changed the developmental process may also be changed. But these external factors may be notably changed in many ways without any corresponding developmental change except, perhaps, retardation or acceleration of the period of incubation of the embryo. We cannot, by any environmental change cause the cod-egg, for

example, to develop into a whiting. Thus it is the " internal factors," that is, the potentialities of the organization, that are specific in nature.

v. It is an intensive manifoldness.

Although we must think of an organism as being one undivided, whole thing our attention analyses it, both in respect of its morphology and activities, into many parts, structures, organs, modes of functioning and behaviour : at all events these are *aspects* of the organism. Since the organization, acting on the environment, becomes these parts, or aspects, we may think of the latter as being in the organization—as the potentialities. Our analyses show us the parts, organs, etc., as being extended in space, laid alongside each other, being dorsal or ventral, right and left, anterior or posterior, etc. : in short, being spatially related. But we cannot discern such spatial relationships in the developmental potentialities, though it may be convenient to think about the latter as manifold. Therefore the manifoldness is intensive, that is, the " parts " of the organization interpenetrate each other. The conception has no difficulties, thus the notes of a musical chord, accurately played, are not spatially or temporally separate from each other though experience enables us to analyse the chord so as to distinguish its constituents.

vi. The developmental organization cannot clearly be thought about as being IN *space but it acts* INTO *space.*

That means that the intensiveness of the organization in the ovum about to develop becomes an extension of parts (blastomeres, anlagen, organs and tissues) that can be measured and given space-coordinates. It is this discontinuity that perplexes us and makes the conception of a developmental agency obscure. By reason of our application of (classical) physical conceptions (matter, energy, etc.) to the embryogenetic process we try to give every developmental phase that can be drawn, measured and physically described a preceding phase that can also be physically described. Thus there were the historic, crude, preformationist hypotheses and now there is the modern geneticist outlook that makes the genes physical things just as characters, organs and parts resulting from the activities of the genes are physical things. But looking at the problem candidly and critically we simply cannot discover anything that " causes " development in the ovum —that is, anything physically extended. What we know is that

there are potentialities in the physical sense. These act so that their results appear to us as things (blastomeres, etc.) physically extended.

We have not been inclined to think about space otherwise than as something indifferent. It is true that the tide-generating force of the moon on the ocean is proportional to the square of the distance of the moon, but we look upon this force as " exerted " by the mass of the moon. But it would appear that what any blastomere, or small mass of cells in an embryogeny, is going to become depends on its spatial relationship to other blastomeres, or cells. Thus the epidermal cells opposite to the developing optic cup become the crystalline lens of the eye and the adjacent epidermal cells remain epidermis. But if the optic cup is " transplanted " the opposite cells in the new region of epidermis (which otherwise would have remained epidermal) now become crystalline lens. At present it is in keeping with modern speculation to say that the cells of the optic cup secrete enzymes which so act on the adjacent epidermal cells as to cause them to become a lens—obviously this is only speculation.

And in recent physics space has acquired positive quality, or properties. This, of course, is only mathematical speculation, still it is suggestive of a corresponding outlook upon developmental problems.

vii. The developmental organization can be indefinitely subdivided and still remain what it was.

Thus a cod-egg may become an adult fish which spawns several millions of eggs and each of the latter may again become a cod and reproduce several millions of eggs and so on without limit. In such a case we must think about the original " single " organization as being divided into millions of parts and of each " part " being again similarly divided and so on. In all these " parts " the original organization is present. There is no limit, because though evolution means a change in the organization (so that a new species of *Gadus* comes into existence) there need not be any evolutionary process. There is no physical analogy to this. In all energies there are quanta, or minimal limits to subdivision. We cannot clearly think about the organization as suffering diminution by subdivision and then growing again, for it is not a material-energetic entity (though it *implies* energy). It has been suggested that there is a physical analogy given by fragment-

ing a crystal, growing the fragment in mother-liquor and again fragmenting and so on : it does not, however, need much acumen to expose the analogy. The only analogous thing is the communication of an idea from one man to another, who then shares it with another and so on.

Driesch's argument, in this connection, still retains its validity. If we conceive of the organization as a material-energetic mechanism we cannot clearly think of anything of that nature that can be subdivided and still remain what it was. And, of course, the self-reproduction of a machine cannot easily be imagined.

76. *ON THE PSYCHO-BIOLOGICAL CONCEPTION OF THE DEVELOPMENTAL PROCESS*

So far as we can understand it, the developmental organization or agency, is (1) not a chemical substance, for this, of itself, would disintegrate into simpler substances and attain equilibrium ; (2) It is not a form of energy, for this, of itself, would undergo dissipation ; (3) it is not anything kinetic, for in the resting ovum that is going to develop there are no chemical or physical activities apart from feeble respiration ; (4) it is therefore a potential—the power to do something which, nevertheless, may not be done ; (5) it is a specific power or potential, that operates upon physical-chemical things so as to produce a unique configuration—the organs and tissue of the organism—and this unique effect is manifested in an indefinitely great number of examples, or individuals of a species ; (6) it is not spatially extended in the ovum, for (7) it can be indefinitely subdivided among the millions of ova formed by the one ovum that develops.

There is no chemical-physical agency known to us that is as we have just seen the developmental agency to be. But every human being (or, at all events, the reader) has immediate and unconfused knowledge of an analogous agency in his own mind. The salient *fact* about the developmental organization is that it assembles things in some specific configuration and that is what the inventor of a machine, the bricklayer, the musician who writes an original theme, the artist in general, or the man who plays a game of " Patience " with a pack of cards does. In all these cases a configuration of some kind is thought about, visualized, imagined or contemplated. Such a configuration does

not, at first, actually exist, but the thought of it, or the mental plan exists, not in space but *involved* in the mind of the worker : it is a potential that is realized spatially in the machine, building, original musical theme, or arrangement of cards. The assembling of the things may be carried out in various ways and there may be limited interferences with the process of assembling that can be " circumvented "—as a developmental process can be regulated should there be interference. The constructive, assembling power of the human mind is not an energy-form but rather the direction and couplings of energies. The mental potential or constructiveness is not in space, for we cannot, without confusion, say that a thought occupies space. This analogy of the developmental agency with the mental operators is the only one that can be clearly made.

It is the obvious and natural analogy to the agency of organic development. It is probably a very old idea : certainly Oken, in 1805, had essentially the conception suggested above. To him development was synthetic and epigenetic. He regarded the ovum as an entire animal in idea and design but not in structure. In it was the future body, not as a corporeal miniature but as " an impalpable spectre." That which was in the ovum was to that which the developed ovum became *as the thought is to the word.*

Essentially the same conception is included in the mnemic hypotheses of Hering, Butler, Semon and others. The developmental organization is of the nature of memory. The developing embryo displays those activities which it would display if it knew what it was doing. " Knowing " here is not consciously knowing, or cognizing, and it is not a misuse of terms to speak of " unconscious knowledge " : obviously an artisan who has learned to perform some highly skilled operations " knows what he is doing," to the degree that he may even regulate his activities should there be interference, but, just as obviously, he may perform these actions automatically, without thinking about them, but perhaps thinking and speaking of something quite different. Obviously the infant that is newly born " knows " how to perform the complex actions of suckling its mother's breast, but these neuro-muscular actions are not performed with that conscious knowledge with which a man " draws " at a pipe that is partially choked up. Knowledge on the part of the developing embryo

is assumed by Butler, but the "knowledge" has the above qualifications. The ovum (which is, in all respects, an organism) has unconscious memory of the development of the animal of which it was a part, and of the development of the parent of that animal and so on indefinitely. Why should it not have such unconscious memory? It is organically continuous, in the most literal sense, with all those past generations. We recognize instincts, which are simply inherited but unconscious knowledge of, or ability to perform, complex tectonic operations. We recognize inherited or ancestral experience. Between these latter conceptions and that of the unconscious tectonic knowledge of the ovum and embryo there seems to be little essential difference. The ovum, then, develops in the specific manner that it does because a very long series of individuals, with which it was organically continuous in time, have developed in this specific manner and the practical knowledge, or ability to perform the embryogeny is much the same thing as, for instance, the knowledge that a bird has of assembling natural materials the first time that it builds a nest—this nest-building being, of course, only the completion of the development of the sexually mature animal. A *habit* has become established in the course of the innumerable individual developments in a race and the recurrence of specific embryogenies expresses this habit. The habit has its basis in the "unconscious memories" of the individuals of the race, that is, in the retention, in some way, of past experiences in a psychic substratum: obviously one may not attempt to be more exact than this.

Why? For the mnemic hypotheses, in its most exact formulation by Semon only reintroduces confusion by its attempt at exactness sought through a physical substratum. In these formulations experiences that involve reception and response are regarded as establishing "engrams," which are actual impressions on, or are physical-chemical modifications of the nerve, germ and somatic cells. All the confusion that results from the attempt to make the developmental organization a physical agency then again attaches to the hypothesis. And Bergson's analyses of the mental and physical phenomena of aphasias does not seem to leave any doubt that memories (images) cannot be in the material-energetic brain. What a cerebral lesion does is, not to destroy a memory-image, but to prevent that image from influencing

behaviour : it destroys, or impairs neurone-configurations (nerve-tracks and synapses) and so also motor habits. But it seems to be certain that the memory-image need not be obliterated.

76*a*. Development—Hypotheses and Practical Investigations. Preoccupation with the psycho-biological conception appears to (though it need not) inhibit the practical investigation, morphological and physiological, of embryogenies. It is not yet a working hypothesis and even if it were its methods would not be physical-chemical ones. Beyond doubt there is immense interest in the details of embryogenies, as studied by the microscope ; in life-histories on the extended scale ; in the physiological and bio-chemical events of a development and in the study of the conditions of the environment. What the minute morphology of the cell-nuclei of germ-cells and embryonic complexes will yet reveal is not certain ; it is possible that the cytology of the future will be a chromosomal physiology instead of a pure morphology, as at present. It is probable that we shall see in these minute systems only the apparatus of assimilation and not that of embryogenic tectonics.

All the more (should it prove true that the embryogeny of an organism is a habit sustained by unconscious memory) may we expect the development of an animal to throw light on the past of the race—on the phylogeny of the groups represented by the animal. That, of itself, would be a result of very great interest since, as we shall see, it may be that the palæontological records of that phylogeny are irremediably destroyed.

CHAPTER VII

HEREDITY

By " heredity " we mean that the progeny of an animal belongs to the same category of organisms as do its parents. This definition is of the nature of a " first approximation " and it will be amplified in the following pages.

77. *ON THE CATEGORIES OF ANIMALS*

Investigations of the structures of living and fossil animals enable us to make a hierarchy of categories : it is necessary, first of all, to base these categories on structural characters so that we may include fossil forms of which we have only (partial) knowledge of structure. Afterwards we may base the categories, so far as possible, upon the habits and life-histories of living animals. The categories are *logical constructions* and they are made by naturalists rather than being " in nature." What we observe in nature are individual organisms and we classify these. Thus while the broad outlines of classifications are generally agreed upon by systematists there is much difference of opinion upon the finer details and these divergences represent not only imperfect inductions but also different criteria as to the formulation of the categories.

A classification is hierarchical. At its base are *species*. Groups of species that have certain characters in common are called *Genera ;* groups of genera are *families* ; groups of families are *Orders ;* groups of orders are *Classes ;* groups of classes are *Phyla* and a small number of Phyla constitute the animal kingdom. But even upon the formulation of the hierarchy there are differences of outlook. All these categories, sub-categories, etc., are plainly logically constructed concepts, but something more must be said about species.

77*a*. Species. These are, to some extent, natural categories in that they are " in nature." The individual animals that

" belong " to the same species often inhabit some restricted region. They all resemble each other more than they resemble the individuals that, we say, belong to other species. They are all mutually and indefinitely fertile with each other if they reproduce sexually and they tend to be immediately or ultimately infertile with the individuals of other species if they reproduce sexually. This statement, also, is a first approximation. Well-known species, such as those familiar to fishermen, sportsmen, gamekeepers, breeders and naturalists have individuality, in a way. There is no doubt at all as to their " specific identity," so that a fisherman, for instance, recognizes " at sight " the species, or kinds of animals with which he deals. Without doubt there is very much confusion in zoological literature as to many of the species made by naturalists upon the evidence of only one or a few badly known specimens and so almost every species has a " synonymy." But here we have obviously to do with imperfect inductions and as knowledge increases the status of the naturalists' species becomes ever more clear.

As natural history becomes more perfect the geographical distribution of the species becomes well known. It is then apparent that a systematic, or " Linnæan " species can be decomposed into *local races*. Thus the Atlantic cod (*Gadus callarias*) is a perfectly definite kind of fish never to be mistaken for any other kind by a fisherman. Nevertheless, the fisherman knows different sub-categories of cod distinguished by geographical prefixes and the naturalists know that there are about half a dozen races of cod distinguished (among other things) by differences in the numbers of vertebræ in the backbone. These races of cod cannot, in general, interbreed with each other and there cannot be much inter-migration between the various sub-regions : otherwise the morphological distinctions between the local races would become obliterated. Generally let there be local races of a systematic species, *a*, *b*, *c*, *d* and *e*, and let these races inhabit contiguous subregions, *a* being near *b*, *b* being near *c* and so on, but *a* being far removed from *e*. We expect to find that *a* will be fertile with *b*, *b* with *c*, *c* with *d* and *d* with *e*, and we also expect to find that *a* will tend to infertility with *e* and, in any case, will not have the opportunity of freely interbreeding with *e*. But not many good investigations of this kind have been made.

As a first approximation we may say that such local races represent natural, irreducible, morphological categories of animals living in the wild. The progeny of the animals belonging to a local race are recognizable as also belonging to that local race. But we shall see that even these local races are also logical categories of organs.

78. *ON HEREDITARY RESEMBLANCES*

We proceed now to qualify the above statement of what we mean by " heredity." It would not be true to say that the parents are " similar " to the progeny. By " similarity " we mean that two things are so much alike that they cannot be distinguished from each other, no matter how carefully we investigate them. This is never the case with regard to parents and offspring : (1) Because parent and offspring are always animals in different *phases* of a life-history and are, therefore, not similar ; (2) there is generally *sexual dimorphism* : the offspring, whatever its sex, is always sexually different from one parent and this difference includes not only the essential sex-organs, ovaries and testes but it may also include external genital organs and un-essential bodily characters (such as hair on the face in men) that go along with sex. (3) There may be *polymorphic castes* : thus the progeny of a queen bee includes females, males and neuters, castes which are well-distinguishable morphologically. So also with ants, etc. Of course, in parthenogenetically and vegetatively reproduced races such sexual polymorphism does not exist. (4) Finally, there are always what we shall call *fluctuations* of morphological character in the individuals of a local race and even in the individuals of the same " brood " or progeny. It does not matter here that these fluctuating differences are " non-inheritable," they are still differences.

Therefore the characters of the parents are not similar to the characters of the progeny, but this does not spoil our statement of what is meant by heredity. (1) Because the definition of the characters by means of which we define a local race, say, is a definition of those characters *at all phases* in the life-history so that, although the young animal may be very different from the adult, these differences are included in the definition of the category. (2) The definition includes both male and female

characters. (3) It includes polymorphism, so that all the bee castes are still regarded as bees. (4) It takes fluctuating variability into account by assigning a certain range to each measurable character.

We see also that all local races of the cod are still the individuals of the specific category *Gadus callarias*. Greenland cod have 51 to 55 vertebræ and Irish Sea cod have 50 to 54: they belong therefore to different categories, or local races of cod. But, from its definition, the species *Gadus callarias* has 50 to 55 vertebræ so that although Newfoundland and Irish Sea cod-races are different from each other they are still *Gadus callarias*—because of the logical schemes of our classifications. When we make the statement:

Characters of parents = Characters of progeny,

which is what we mean by "heredity," we are not making an equation but what the mathematicians would call an identity.

What we study in heredity are the ways in which the progeny differ from the parents (if they differ), what regularities can be found when we study these differences and how we can control breeding so as to minimize or maximize these differences, or bring them under control. These problems are different ones according to whether the modes of reproduction of the organisms concerned are vegetative, or asexual, or parthenogenetic, or sexual. In vegetative reproduction the new organisms are, say, plants that are multiplied by grafts, slips, cuttings, etc., and not by seeds. In many cases animal organisms (such as some protozoa) multiply by simple fission, without conjugation. In parthenogenesis the animal reproduces by means of ova which are not fertilized (since there are no males). When there is not amphimixis the problems of heredity (apart, of course, from *the* problem of development) are relatively simple. Any species that does not reproduce sexually may be regarded as being constituted by a number of "pure races" and it may be possible to isolate such categories. Without going into detail upon this part of our subject it may be sufficient, in the meantime, to regard pure races in asexually reproducing organisms as being the descendants of one original ancestral organism. When we study heredity in sexually reproducing organisms the problem becomes much more difficult.

79. *ON HYBRIDITY*

A hybrid organism is the offspring of male and female parents that belong to different categories. (Again the definition is of the nature of a first approximation and it will be qualified and amplified in the following sections.) Let there be a hierarchy of categories :

order, *family*, *genus*, *species*, *local race*

and it will be found that there is a boundary somewhere such that the individuals belonging to the categories on either side of the boundary are infertile with each other. Usually the individuals of a local race are fertile with those of other local races that are included within the same species, but usually the individuals belonging to a species are infertile with those of other species that belong to the same genus. We may, to begin, draw the boundary between the categories, genus and species, but it is not impossible that individuals belonging to different genera may be fertile with each other. This is exceptional, but evidently the place of the boundary is obscure.

The obscurity of the boundary is due to what may be called " physiological reasons " (though the statement is unilluminating). It is the case that the definitions of the categories are obscure since they have been based on morphological and not on physiological criteria. Thus we may postulate that all the individuals of a species are to be regarded as interfertile, so that if we observe that the individuals are infertile the conclusion is that they belong to different species. This means that we include infertility with other categories as a part of the definition of a species and such a criterion cannot be applied to the majority of the species of the classifications, for we do not know what are the facts with regard to most of these formal categories that live in the wild and have not been domesticated, or made the objects of experiment. There may even be infertility between the individuals that belong to the same local race and it is known that wild animals may not breed when kept in captivity.

79*a*. Immediate and Ultimate Sterility. In general the individuals of different well-known species that live in the wild state are sterile with each other. It is said that there are " instinctive antipathies " (as between dog and cat), or anatomical reasons (such as mere differences in size), why such specifically different

animals may not copulate. But where the fertilization of the ova may be a quite promiscuous affair there may still be infertility between individuals belonging to different species. Thus the eggs and spermatozoa of cod, haddock and whiting may be spawned into the same restricted part of the sea and fertilization may occur in the water and outside the bodies of the parent-animals. We might expect, in such a case, that the sperms of, say, cod, would sometimes fertilize the ova of whiting, but undoubted hybrids between these and other species of Teleostean fish that reproduce in this way are practically unknown. It is also known that artificial impregnation of the ova of one kind of fish by the spermatozoa of another kind may result in the segmentation of the ovum, but rarely in a developmental process that proceeds so far as the hatching-out of the embryo. Therefore there must be physiological reasons for the infertility.

If no offspring results from the crossing of individuals belonging to different categories we say that these crossings are immediately sterile. If hybrid offspring do result from such crossings and if these hybrids are sterile animals we say that the original crossings are ultimately sterile. If the hybrids are fertile with each other for a number of generations but if the strain tends to die out there is again ultimate sterility. The matter may be very complicated : thus European men are fertile with Negro women and the mulattoes and mulattresses so produced are fertile with each other and with individuals belonging to the parent (European and Negro) races. But the mulattress crossed with the mulatto is said to have few children and to abort easily so that this strain tends to die out, the crossing, *mulatto* × *mulattress*, being ultimately sterile. On the other hand, the mulatto and mulattress when crossed with individuals of either of the parent races are immediately and ultimately fertile, for the strain persists, though it tends continually towards a parental racial strain. When the original Dutch colonists settled in Java a race of hybrids (with the native women) came into existence. These " Lipplappen " are said to have been immediately fertile with each other, but such crossings resulted in the births of girls only and these girls were sterile. Therefore the original crossings were ultimately sterile.

79*b*. THE SIGN OF THE CROSSING. It matters which way the cross is made : *male A* × *female B* is not the same thing as *female B* × *male A* (*A* and *B* being different categories). Thus the cross

mare × *male ass* gives the hybrid mule, but the cross *female ass* × *stallion* gives the hybrid Hinny, which is a different kind of animal. Similar results may come from the crossings of cage birds and the sign of the crossing may even affect the fertility itself.

80. *ON MENDELIAN HYBRIDITY*

It will be convenient to speak of " Mendelian categories " and these are best illustrated by the results of the classical pea-experiments. The plant, *Pisum sativum*, is a systematic species defined by an ensemble of morphological characters which we shall call *E*. But this specific category can be split up into finer ones, each defined by certain special characters, or small ensembles of characters, that distinguish it from the others. Thus the pea-plants may be tall ones (*t*) or dwarf ones (*d*). They may bear peas that are green (*g*), or yellow (*y*), or round (*r*), or wrinkled (*w*). Thus we may have categories : pea-plants with the characters, *E*, *t*, *g*, *r* ; *E*, *t*, *y*, *r* ; *E*, *d*, *g*, *r* ; *E*, *d*, *y*, *r*, etc. That is, there are combinations of the special characters (*t*, *d*, *y*, *g*, *r*, *w*) that define each category, but *all the categories exhibit the ensemble E*. Later on we shall speak of the characters of the ensemble as being " integrated " ones and of the special characters as being " loose " ones. Mendelian stud es deal, *first*, with the results of crossing different Mendelian categories, and, *second*, with associated cytological results.

Pea-plants can be bred by cross-fertilization, the pollen of *A* fertilizing the ovules of *B*, or *vice versa*. Or they can be self-fertilized (" selfed ") when the pollen of *A* fertilizes the ovules of *A*.

Typical experiments. We consider only two characters, yellowness of the peas and greenness of the peas. (1) When a plant that is known to bear yellow peas only is crossed with a plant that is known to bear green peas only a Mendelian hybrid is produced. This hybrid bears only yellow peas, but it has also the potentiality of green peas. The character (*y*) is said to be " dominant " over the character (*g*), (which is called " recessive ").

(2) The yellow peas from this experiment are sown and plants are raised from them. These plants are then selfed and allowed to bear peas and it is found that about one-fourth of all the peas that they bear are green and that about three-fourths

are yellow. The character *g* is thus separated from the character *y*.

(3) The green peas obtained as in (2) are now sown and raised to plants and the latter are selfed. All the peas that they bear are green ones. If these peas are again sown, and if the resulting plants are selfed, all the peas that they bear will be green ones and so *ad infinitum*. Thus a Mendelian " Pure race "—" pure " in respect of the colour of the peas, is obtained.

(4) The yellow peas obtained as in (2) are sown and raised to plants and the latter are selfed. They will bear both yellow and green peas : one-third of all the plants bearing yellow peas and two-thirds bearing both green and yellow peas. The yellow-peaed plants of the one-third fraction are a " pure race " (as in (3)) in respect of yellowness, but the two-thirds fraction, when sown and grown and selfed, will again bear both yellow and green peas.

From these simple experiments we can make certain provisional conclusions :

(*a*) In hybridizing Mendelian races of pea-plants the ensemble of systematic, or specific characters, *E* appears unchanged in the progeny.

(*b*) In hybridizing Mendelian races of pea-plants we can obtain progeny that display only one of the two characters of the races but have the potentialities of displaying, in their progeny, the other character (the " Principle of Dominance and Recessiveness ").

(*c*) In such progeny that display a dominant character but have also a recessive, or potential one, further breeding can result in progeny that display both characters (the " Principle of Segregation ").

(*d*) There are pairs of characters (green peas and yellow peas, tallness and dwarfness, round peas and wrinkled peas and so on). If one of a pair of characters is displayed the other one is not displayed. The pair of characters are called allelomorphs. (This is the " Principle of Allelomorphism.")

Proceeding in the same way we can hybridize pea-plants that have 2, 3, etc., pairs of allelomorphic characters. Thus there may be yellow peas that may be round or wrinkled and green peas that may be round or wrinkled. There may be tall pea-plants that bear green peas that may be round or wrinkled, dwarf pea-plants that bear green peas that may be round or wrinkled and so

on. If there are the 3 pairs of allelomorphic characters, *a* and *b*, *c* and *d*, *e* and *f* we can have these combinations,

ace, *acf*, *ade*, *adf*, *bce*, *bcf*, *bdc*, *bdf* (*or* 2^3 *in all*),

and if there were *n* pairs of characters we might conceivably have 2^n combinations. Thus we see that, *so far as we have gone* the notion of randomness enters into Mendelian theory, that is, the above combinations, *ace*, *acf*, *ade*, etc., are the possible assortments when we take one out of each pair of characters and associate them at random. But the randomness may be restricted. Thus some men see badly in the dark in conditions when normal men see relatively well, and this is called night-blindness. When a normal woman has children by a night-blind man all these children (boys and girls) have normal sight, but if the girls grow up and have children by normal men some of their sons may be night-blind. Women are said not to be night-blind, but they " carry " the character night-blindness, so that the latter is said to be linked with sex (the " Principle of Linkage ").

This very slight summary of Mendelism notes the aspects of the subject that have general interest. There is, of course, very much more, but much of it is perplexing, is loaded with detail that is irrelevant from our point of view, is contradictory and may (without loss) be neglected. The " principles " must all be qualified by subsidiary principles : thus there is " imperfect dominance," imperfect segregation (as in sex-linked characters), multiple allelomorphism, etc. Thus maleness and femaleness seem to be allelomorphic characters, but there may be hermaphroditism in animals in which the sexes are usually separate and there may be " intersexes," when the male shows some of the morphological characters of the female, and *vice versa*, and animals (hens) that are female when young may show male characters (hens will crow) when they become old. Such refinements, and subsidiary hypotheses " accounting " for them, may be neglected. Later we shall consider the theoretical interest that Mendelism has for general biology.

81. *ON THE CYTOLOGICAL PHENOMENA ASSOCIATED WITH MENDELIAN HYBRIDITY*

In the first discussions of what we now call Mendelism it was assumed that there were agencies in the ova and spermatozoa that were the causes of the appearances of the characters and these

agencies were called " factors " : thus there were factors for the greenness of the peas, the yellowness of the peas, the tallness of the plants, and so on. Later on there were supposed to be single or double " doses " of a factor, there were " enabling," or qualifying factors, etc. Factors were said to be coupled and so on. When the appearance of a character could not be " explained " by a single factor such subsidiary hypotheses were made. Such results as we have considered came from actual breeding experiments, but in their interpretation the factorial hypotheses were made. Now from what has already been said as to the nuclear phenomena in germ-cells it will be seen to have been inevitable that the results of breeding experiments should have been associated with the results of cytological investigation of germ-cells. And, after Weismannism, it was inevitable that particulate things, or agencies, in the chromatin of the germ-cells should have been identified with the Mendelian factors. Thus instead of factors we now speak of " genes " and these *are*, or are associated with, units of chromatic, nuclear substance. We must now consider what appear to be the results of cytological investigation that are relevant in this respect.

81*a*. The Maturation of the Germ-cells. The cells of the gonads that are going to become ova and spermatozoa are generally regarded as the descendants of original cells in the embryonic gonad-anlagen that have persisted into adult life in the undifferentiated state. (But it may be that peritoneal cells of the adult body may also become germ-cells.) Either a relatively small number of gonidial cells (in the late embryo) serve throughout life as the cells that are going to become ova, or, every year, these cells proliferate (or reproduce) so as to become millions (perhaps) of ova that are annually " spawned." In all cases there is a continuous (or annually recurring) proliferation of cells that are going to become spermatozoa.

Before the gonidial cells become ova or spermatozoa they undergo " maturation." Each cell has a certain number, N, of chromosomes. Each gonidial cell may enlarge and changes occur in its chromosomes. The latter may bunch up, extend out into a long thread, disintegrate into granules, etc. In spite of their disappearances and reappearances there is said to be a " continuity of the chromosomes." This is necessary to genetic hypotheses, but since the chromosomes are actually nucleo-protein,

and since this substance is repeatedly hydrolyzed by enzymes, or otherwise becomes chemically transformed, it must be the agencies that reassemble, or resynthesize the chromosomes that are the continuously existing things.

We assume that there are N chromosomes in the gonidial cells. Now such a cell is a direct descendant of the fertilized ovum, which has half (or $\frac{1}{2}N$) chromosomes that have been derived from the male parent and $\frac{1}{2}N$ from the female one. In an imaginary case let us say that the gonidial cell, about to mature, has 8 chromosomes and that half of these, $A\ B\ C\ D$, are of paternal, and half, $a\ b\ c\ d$, are of maternal origin. The gonidial nucleus, then, contains the chromosomes, $A\ B\ C\ D\ a\ b\ c\ d, = N$. Now, in all the cell-divisions between the phase of the fertilized ovum and the gonidial cell, and in all the cell-divisions by which one gonidial cell becomes many gonidial cells, the chromosomes are always halved and so we conclude that every gonidial cell about to mature has equal numbers of chromatic units derived from paternal and maternal parents.

There is evidence that *either* the paternal group, $A\ B\ C\ D$, or the maternal group, $a\ b\ c\ d$, is a competent agency in the development of the Mendelian characters. (It is true that we have to postulate an ensemble of agencies, or an agency, E, to explain the development of the specific characters, but we do not consider this ensemble here.) When $A\ B\ C\ D$ is the developmental agency (with regard to the " loose " Mendelian characters) the paternal characters are reproduced : conversely $a\ b\ c\ d$ reproduce the maternal characters. There is evidence that if one chromosome is missing (say there is only $A\ B\ C$, or $a\ b\ c$) the development will be imperfect. It is assumed that whatever A does a will do much the same and so on (except that A gives the paternal bias and a the maternal one). So a normal embryo will come from $A\ b\ C\ D$, $a\ b\ C\ D$, $a\ B\ c\ D$ and so on (though there will be mixtures of paternal and maternal characters). We may call A and a, B and b, etc., " homologous " chromosomes. We may further call " A," " B," " C," " D " a " developmental outfit," where " A " may be either A or a, " B " may be either B or b and so on.

Now when maturation occurs N chromosomes are reduced in number to $\frac{1}{2}N$ and this is assumed to be the result of the coupling, in pairs, of the N bodies. This coupling is believed

not to occur at random (if it did so the whole hypothesis would be spoiled). We have, before maturation, $A\ B\ C\ D\ a\ b\ c\ d = N$, and after the coupling we might have $A\ B$, $a\ C$, $D\ d$, $b\ c = \frac{1}{2} N$. But there is some evidence that the pairing (synapsis) has tendency —that " homologous " chromosomes come together, thus : $A\ a$, $B\ b$, $C\ c$, $D\ d = \frac{1}{2} N$, and there is also some evidence that the next process, that of *disjunction*, is also a tendential one. At this phase the gonidial cell-nucleus contains the 4 *haploid* chromosomes, $A\ a$, $B\ b$, $C\ c$, $D\ d$, each of them formed by the joining of homologues. Either now, or even earlier, each *diploid* chromosome splits into 2, thus—$\frac{A\ a,}{A\ a,} \frac{B\ b,}{B\ b,} \frac{C\ c,}{C\ c,} \frac{D\ d,}{D\ d,}$ so that what we really have are 4 " tetrad " chromosomes. We visualize the nucleus as in 1, Fig. 30.

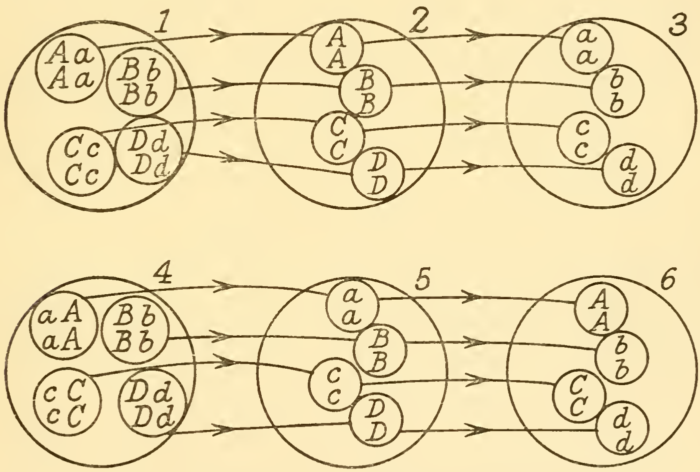


FIG. 30.—DIAGRAM OF THE MATURATION DIVISIONS.
1, Gonidial cell about to divide heterotypically to form (2 and 3), the dyads.

What follows is called the " heterotypic " division. Each tetrad divides into two parts :

$$\frac{A\ a}{A|a} \text{ becomes } \frac{A}{A} \text{ and } \frac{a}{a},$$

$$\frac{B|b}{B|b} \text{ becomes } \frac{B}{B} \text{ and } \frac{b}{b}$$

and so on.

As the nucleus divides one-half of each tetrad goes into each daughter-nucleus.

Now it is a matter of chance which way the tetrad is situated in the mother cell before the heterotype division occurs. Thus we may have the divisions 5 and 6 (in Fig. 30).

Here we have two cases: the " *A* "s in the first case (2) are $\frac{A}{A}$ but in the second one (5) they are $\frac{a}{a}$ and so on. Thinking over the matter the student will find that there are sixteen ways in which (by random now) the nucleus containing the tetrads can divide so that each daughter-nucleus receives an " out-fit," " *A* " " *B* " " *C* " " *D*," but the outfits will differ from each other in that they contain different combinations of maternal and paternal chromosomes.

The dyads now divide just as in an ordinary mitosis, thus:

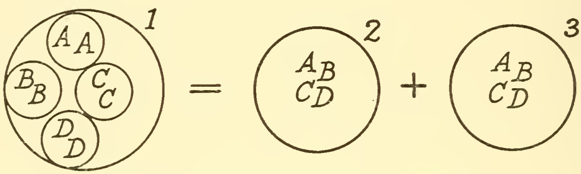


FIG. 31.—DIVISION OF A DYAD.

and each gonidial cell will thus give rise to four daughters. If the gonidial cell is an ovum-mother-cell one of the daughters becomes the ovum and the other three become the (abortive) " polar bodies." If the gonidial cell is a sperm-mother-cell all four daughters become functional spermatozoa.

81*b*. THE GAMETES. The gametes are the cells that conjugate, the ova and spermatozoa. It will be seen from the above summary account of maturation that there are (if the haploid number of chromosomes is 4) 16 different kinds of ova and as many kinds of spermatozoa. There are, for instance, the ova, *A B C D*, *a B C D*, *a b C D*, etc. All these kinds of ova (and spermatozoa) contain the developmental ensemble *E* and the " outfit " " *A*," " *B* " " *C* " " *D*." The ensemble *E* is (by hypothesis) the " outfit " that is responsible for the development of the specific (and constant) characters and the " outfit " " *A* " " *B* " " *C* " " *D* " is responsible for the development of the " loose " Mendelian characters.

Conjugation of the gametes. It is a matter of chance which kind of ovum conjugates with which kind of spermatozoon. Thus :

$A\ B\ C\ D + A\ B\ C\ D = A\ B\ C\ D\ A\ B\ C\ D$ (all paternal)
$a\ b\ c\ d + a\ b\ c\ d = a\ b\ c\ d\ a\ b\ c\ d$ (all maternal)
$a\ B\ C\ D + A\ b\ c\ d = a\ B\ C\ D\ A\ b\ c\ d$ (mixed characters from both parents.)
$a\ b\ C\ D + A\ B\ c\ d = a\ b\ C\ D\ A\ B\ c\ d$ do.

and so on through 256 arrangements.

Therefore hybridity " rings the changes," so to speak, on these " loose " character-components.

81*c*. " Crossing-over " of the Chromosomes. We have considered only a small number of characters that can so be rearranged when mutually and indefinitely fertile races cross. We take only 4 (haploid) chromosomes and, for simplicity, we assume that each of these " carries " a factor that is responsible for the appearance of a character. But there may be about 200 characters in a species (Drosophila) and there are only 4 chromosomes, so it appears that each of the latter must " carry " many characters. The hypothesis (founded on evidence) is that a chromosome carries a group of " linked " characters. Where there is sexual mating it is such grouped characters that " go into the cross." Thus instead of assortments and reassortments of *single* characters (as in the above schemes) there may be assortments and reassortments of " linked " or grouped characters, for instance, when night-blindness is " linked " with maleness (in men). Now we must consider the conception of

Genes. There are, we suppose, only 4 chromosomes but there may be (say) 150 characters that can be observed to behave in the Mendelian way. It can often be seen that a chromosome is made up of a single, or double row of granules. This has suggested that there are hypothetical counterparts, in the chromatin of the ova and spermatozoa, of the adult bodily characters. We cannot actually see these things that are the counterparts, but they are supposed to be present in the chromosomes as entities called genes. In the case of the fly, *Drosophila*, chromosome maps have been made to show the distribution of the genes in the latter structures and it is an essential part of Mendelian hypothesis that the genes are arranged linearly.

Let *a b c d e f g h* be such a row in one chromosome and let another chromosome carry, or be composed of an analogous series, *i k l m n o p q*. When synapsis occurs homologous chromosomes pair, so that the conjoined structure may thus be represented, $\frac{a\ b\ c\ d\ e\ f\ g\ h}{i\ k\ l\ m\ n\ o\ p\ q}$. Now disjunction occurs in the reducing division and the two rows of genes come apart again, but before this occurs it may happen (and there is said to be evidence that it does happen) that the two mating chromosomes become partially twisted round each other (1).

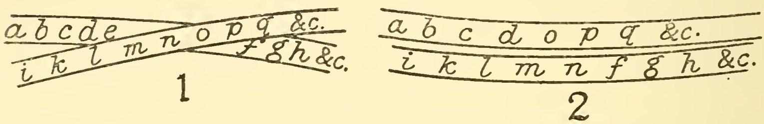


FIG. 32.—DIAGRAM OF THE EVENTS IN A SIMPLE "CROSSING-OVER" OF THE CHROMOSOMES.

In coming apart, in the disjunction, (2) the chromosomes may break where they cross over each other and the result will be as in 2, Fig. 32. Apparently the twisting of the chromosomes, and their subsequent breaking apart are events that occur at random and it will be seen that the linkages of groups of genes are events that occur at random. It will be seen also that by regarding the chromosomes as linear arrangements of genes, each of the latter being responsible for the development of a single character, the number of possible reassortments of Mendelian characters may be greatly increased. This will also be a consequence of the crossing-over of the chromosomes. And if the very simple scheme of crossing-over just indicated should prove insufficient to account for the reassortments we can have a double-twisting, a "4-fold chiasma," and so on.

81*d*. THE GENES. It will be seen that the cytological investigations enable geneticists to make a correlation between (1) events that occur in the nuclei of the germ-cells and (2) the events that occur when organisms that belong to different races (or show slight differences in their morphology), and that are mutually and indefinitely fertile with each other are crossed by sexual mating. It is inferred from this correlation that entities that are called genes are in the nuclei and that these entities are causal agencies

in the development of the characters that are represented by the small differences in the morphologies of the mating parents. For each morphological character (as above defined) there is a gene in the ovum (or spermatozoon) of a parent. If the gene is not there no corresponding character will develop. Yet the development of such a unit-character requires, not only its corresponding gene, but all the other genes. And, of course, it requires also the " external " factors " of the environment. The cruder Mendelian speculations regard the genes as material particles, thus : " If we magnified a hen's egg to the size of the world (which would make atoms rather larger than eggs and electrons barely visible) we could still get a gene into a room and probably on to a small table " (though the more cautious expressions do not suggest this). We have already seen that it is very improbable that a material-energetic system, *of itself*, can be regarded as a causal agency in a developmental process.

Consider the " chromosome-maps " of the fly *Drosophila*, as drawn by Morgan. All the chromosome material is divided up into the *loci* of the genes *of the Mendelian characters*. Thus there is no mechanism (of genes) in the nuclei that accounts for the development of the specifically morphological characters—there is, apparently, no ensemble *E*. Morgan and his pupils indeed disclaim that their hypotheses involve, in them, a hypothesis of development. Yet it is clear that these hypotheses do involve a hypothesis of development of the loose Mendelian characters *or* they may frankly ignore the problem of development and merely state *how* the characters of parents, that differ slightly from each other reappear in the progenies. Genetics may thus be a study *only* of the reappearances, rearrangements, etc., of the differences of the parents in the offspring.

82. *ON THE ESSENTIALS OF MENDELISM*

(1) Organisms reproduce sexually and all the specific characters of the parents reappear in the progeny.

(2) But there are always slight differences (that are " inheritable ") between the parents in respect of their morphologies. Every such slight difference (blue eyes in one parent and brown eyes in the other) is regarded as a " unit-character."

(3) These differences " go into " the sexual crossing (*via* the

fertilization of an ovum by a spermatozoon). They " come out " from the crossing just as they went in. They are to be regarded as discrete, atomistic, character-entities, just as the atoms of chemical substances are discrete entities. The atoms enter into various combinations with each other in the course of the reactions of the " parent-substances," yet they retain their individualities throughout all the reactions. So the atomistic, Mendelian characters retain their individualities although they may be assorted and reassorted in the course of the matings of the parents and among the progenies.

(4) Most of these assortments and reassortments occur at random : thus the disjunctions of the chromosomes that undergo synapsis ; the reassortments of the genes in the reduction divisions ; the combinations of different gene-complexes in the fertilizations and the phenomena of crossing-over. In conceiving this randomness we are moving away from the essential conception of life—which is anti-randomness.

(5) And, therefore, Mendelian speculation is forced to postulate anti-randomness *somewhere*. We find this in the conception of synapsis of homologous chromosomes—a very difficult problem. Perhaps we find it also in the notion of linkages—so far as this is not accounted for by the crossing-overs.

In the following chapter we shall return to the subject of Mendelian heredity, in so far as it touches upon the problems of transformism.

83. *ON HEREDITY IN GENERAL*

There is no working hypothesis of heredity, for a hypothesis of heredity is necessarily a hypothesis of development. We say that the offspring belongs to the same specific or racial category as did its parent, and this is because the specific developmental process by which an ovum became the parent is the same process by which an ovum derived from the parent becomes the offspring. We say that the specific developmental processes are " the same," neglecting those small, random deviations that we shall call " fluctuations " (Section 84*b*). Now we can divide up the specific, or racial category into sub-categories that we call Mendelian ones. Each Mendelian category displays the specific or racial characters, and, in addition to these, certain trivial characters, or combina-

tions of trivial characters. It may happen that the male and female parents that mate display different trivial, or Mendelian characters, but the definition of heredity given here is not thereby invalidated—among the offspring, or the offspring of the offspring of these parents, will be individuals that display not only the specific or racial characters but also the trivial, or Mendelian characters of one or other parent. Therefore the *whole* developmental process by which two ova became two parents are the same processes by which some offspring become individuals of one parental category and other offspring become individuals of the other parental category.

And the hypothesis by means of which we (provisionally, and for expository reasons) " explain " the " transmission " of Mendelian characters is that the specific developmental process is the result of operation of an ensemble of causal agencies, E, all these being integrated so as to be one agency, while the developmental process that leads to the appearance of a Mendelian character is due to the result of operation of another agency not integrated into the ensemble but capable of being " loosely attached " to the latter. That is the reason that, among the progeny, there may be individuals displaying many combinations of the loose, Mendelian characters displayed by the two parents. Of course, this is not a working hypothesis of Mendelian developmental processes since it does not attempt to investigate the nature of the ensemble, E, or of the developmental agencies that are responsible for the appearances of the Mendelian characters.

83*a*. THE " TRANSMISSION " OF CHARACTERS. It is only for convenience that we say that the parent " transmits " certain characters to the offspring. Consider the very simplest case of a racial history—that of a protozoan that reproduces by simple fission. That the mode of reproduction is asexual makes consideration of what happens simple. Sex only complicates the discussion without changing the essential ideas.

Here we start with the " mother-cell " (or organism), F_0 (Fig. 33). This divides (or reproduces), giving rise to the " daughter-cells," F_1, F_1. F_1 again divides, giving rise to the granddaughter cells, F_2 F_2 and so on. There is, of course, a short phase of development after each division during which the nuclear constituents of the daughter, granddaughter, etc.,

cells reconstitute themselves and during which these and the cytoplasmic constituents grow.

Consider one lineage. F_0 (which we suppose is a protist) divides into the daughters F_1 and F_1. In the act of division F_0 disappears, for it becomes F_1 and F_1. Consider F_1 (one of the daughters). In the act of dividing into F_2 and F_2 the organism F_1 disappears—and so on. In a direct lineage, where the chain is a series of single organisms (the chain being spaced-out in time) the appearance of one generation is simultaneous with the disappearance of the parent. The various things represented by

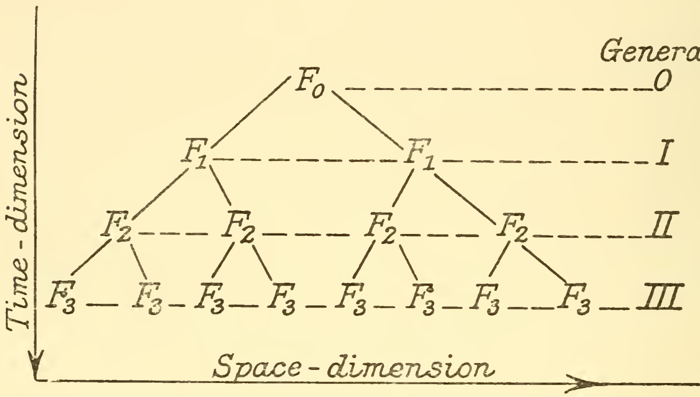


FIG. 33.—GENERATIONS IN SPACE AND TIME.

the "generations" O, I, II and III, are phases in a life-career and the whole series of individuals are obviously continuous in the time-dimension. They are *extended* in a time-dimension that has sign, that is, that proceeds from earlier to later. They are extended also in space-dimension, that is, they have extension in a dimension that has no sign, or passage. Clearly, then, nothing is "transmitted" from one generation to another one, for one generation simply becomes the next one in the time-dimension. If transformism (or "evolution") occurs in the course of the passage O ⟶ I ⟶ II ⟶ III ⟶ etc., there is simply *novelty* in the career.

83*b*. SOMA AND GERM. It is only when our interest centres in the soma, or body, that we have the notion of "transmission of hereditary qualities." When we deal with protist organisms

soma and germ are the same cell. When we deal with animals that reproduce by fission of the adult body, or with plants that reproduce by buds, grafts, cuttings, etc. (that is, vegetatively and without seeds), soma and germ are again the same thing. But when we deal with the multicellular animal we make a distinction between the " body " that is motile, sensory, perceptive, cognitive, etc., and the germ (or gonidial cells) which are reproductive. And even then the distinction may fail because even the " body " may be reproductive of a new (functional or abortive) body. What confuses us is the process of development whereby the germ-cell of the multicellular organism (which is nevertheless the organism) grows and differentiates and displays activities that were only potential in it as a germ-cell. We say, then, that these displayed activities have been " transmitted " from the parental body, *via* a germ-cell to the progenal body, but we really mean that those activities, patent to the parental body, become potential in the germ-cell and then again patent in the body that develops from that germ-cell.

CHAPTER VIII

TRANSFORMISM

By transformism we mean that some of the individuals of a naturally occurring category of organisms undergo changes in their morphology, such that the definition of the category no longer describes them. In this statement we necessarily (but provisionally) restrict the conditions of the problem. (1) We must, first of all, consider naturally occurring categories of organisms because we have to apply the conception of transformism to organisms living in the wild and apart from deliberate human control and (2) we must mainly consider the structure, or morphology, of organisms because we only know the structures of most of the organisms that lived in the past. It will be necessary, of course, to consider also the results of domestication of plants and animals, and it is also necessary that we consider the changes of organic functioning and behaviour that are, in a way, expressed in changes of morphology.

84. *ON CATEGORIES OF ORGANISMS*

We can form really clear ideas of the categories, species and local races and it is from these that we start our discussion. Resuming what has been said before (in Section 77*a*) we note that a species is a group, or category, of organisms such that all the individuals resemble each other more than they resemble the individuals of other categories. Thus well-known species can always be easily recognized. Further, the individual organisms belonging to the same category are immediately and ultimately fertile with each other. *Local races* are categories within the species such that the individuals belonging to one of them resemble each other more than they resemble the individuals belonging to other local races. The organisms in all the local races of a species are usually immediately fertile with each other, though the ultimate interfertility of the individuals of different local races

may be a matter for investigation in each case. The individuals of the local races (in the well-known examples) can always be recognized as belonging to the same species. Thus the North Atlantic cod (*Gadus callarias*) can always be immediately recognized as cod, but there are the races, *Greenlandicus*, *Hibernicus*, etc., and these are seen, upon inspection, to be cod that differ from each other in some details of morphology. Further we know that there is local segregation : that is, Greenland cod, for instance, do not migrate into the Irish Sea and *vice versa*.

In what follows we consider the local races, presuming that a species has usually these sub-categories.

84*a*. Organic Variability in General. What we actually find *from mere inspection* is that the individuals of a local race are not similar to each other in all the details of their structure. Thus Greenland cod have 51 to 55 vertebræ in their backbones whereas Irish Sea cod have 50 to 54. If we examine a large number of fish we find that the variability in respect of the structural character, *number of vertebræ*, has a certain form in the case of each local race. Thus samples of Greenland and Irish Sea cod were obtained and the figures in the tables (frequencies) show how many fishes in a sample had 50 vertebræ, 51 vertebræ, and so on.

Greenland cod.

Frequency of occurrence of N. . .	1	35	119	58	9
N = number of vertebræ . . .	51	52	53	54	55

Irish Sea cod.

Frequency of occurrence of N. . .	5	62	114	11	1
N = number of vertebræ . . .	50	51	52	53	54

These series of figures are " frequency distributions." In each of them we see that the character, " number of vertebræ," is variable. It may be from 51 to 55 in the first case and from 50 to 54 in the second one. These values express the " range of variability," but it will be seen that the range is not quite the same in the two examples. It is customary to graph such frequency distributions as shown in Fig. 34 on page 244.

The individual organisms that vary in respect of some structural character are called *variants* and we see that 5 variants, all exhibiting the same number of vertebræ, are placed in Class 50, 62 in Class 51, 114 in Class 52 and so on. The class that contains the greatest number of variants is usually near the mean value of variable character. Thus the mean number of vertebræ in

Greenland cod is 53·18 and it will be seen that there are 119 variants in the class 53, that is the class nearest to this mean value.

Now when we merely observe, but do not make experiments upon naturally occurring populations, or races, of organisms we see such crude variability, in respect of all structural characters that can be measured. We can, in nearly all cases, represent this observed variability by such frequency distributions and graphs as have been instanced above.

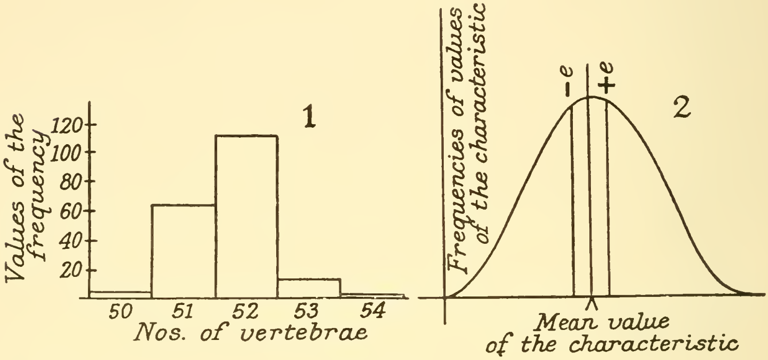


FIG. 34.

1, A histogram; 2, a frequency curve.

84*b*. THE ANALYSIS OF CRUDE, ORGANIC VARIABILITY. However, it is possible to make analyses of the variability by subjecting organisms to domestication, by selecting them, cross-breeding and inbreeding them, etc.—in short, by exercising control over their habits of reproduction and life in general. It is only practicable to do this in the cases of organisms that may reproduce freely in the artificial conditions of the garden, farm or laboratory, and not many cases of crude organic variability have been examined in such ways. But it is permissible to extend (with caution) the relatively few results that have been obtained to variability in the cases of populations living in the wild state.

We distinguish, in the crude variability discovered by inspection, the following kinds of variants:

(1) Mendelian variants;
(2) Mutants;
(3) Random fluctuants and
(4) Fluctuants by acquirement.

Mendelian variants. We have seen that the plants of *Pisum sativum* that are grown in a garden may be tall or short, may bear green *or* yellow, or green *and* yellow peas, etc. We may, then, see a pea-plant that bears yellow peas that are round and which is tall: this is a Mendelian variant and the variable characters are relative tallness, relative shortness, greenness of peas, roundness of peas, etc. It is to be noted that we cannot represent one of such characters, say greenness, as a frequency distribution, that is, there is only (in the classical Mendelian theory) one shade of green, and not many shades, each with its own frequency of occurrence. But in the later elaborations of Mendelism, instead of one kind of character having a nearly constant value (say intensity of colour, or shade of colour), and due to one factor, there may be many intensities, or shades, which are due to the operation of "multiple factors." In such cases the variants may be arranged in frequency distributions such as we have mentioned above.

Apart from such reservations the variations that we call Mendelian ones appear in the individuals that we select for study, and in some or all of the progeny of these individuals, or in some or all of the progeny of the progeny and so on. They assort and re-assort themselves in the hybridizing and other breeding experiments that we make: that is, they are hereditary characters appearing in a racial career in the Mendelian manner. The individuals displaying them are "Mendelian variants." Later on we shall discuss *categories* of Mendelian variants and their possible significance in racial transformism.

Mutants. If we have much experience of the individuals of a racial career we may observe *novelties* in that career. That is, we may discover individual organisms that display some new character—or, at least, some character which has not been seen before, in all the individuals belonging to the race in question, that have been studied. Such a novelty of structure is called a "mutation." Thus, after very many collections of the sand-hopper, *Gammarus*, had been observed one individual was seen that had red eyes: the ordinary *Gammarus* has brown eyes. It is, of course, impossible to be sure that there had never, previously, been *Gammari* with red eyes, but we may assume this, or at least we may assume that if there had previously been red-eyed *Gammari* that race had "died out." Now the red-eyed amphipods

so found were originally mutants. They were bred with brown-eyed amphipods and the red eyes reappeared in the progenies and the progenies of the progenies, in the Mendelian manner, so that, after the original appearance of the mutation red-eyed *Gammari* were regarded as Mendelian variants. This notion of real novelties of structure, or of the appearances of mutants, is essential to any working hypothesis of transformism that we can make. Later we shall consider the conception in greater detail.

Random fluctuants. The mere form of a frequency distribution, such as those that we have studied above, suggests the notion of random variation. We can best illustrate this notion by regarding the results of operation of some process, or mechanism, that is designed to produce things that are intended to be replicas of something, say, a minting machine that produces coins that are expected to be of the same weight and form. Such similarity of product cannot be attained and if a number of the coins are precisely measured it is always found that the individuals fluctuate in weight, etc., round about some mean values of the characteristic that is measured. There will be a small range of values,—e to mean, and mean to $+ e$ (see Fig. 34, 2). The number of individuals that display this small range of values of the characteristic will be greater than the number of individuals that display any other equally small range of values. The number of individuals displaying any similar range of values is less the further removed is that range from the mean, or central range. Such a frequency distribution is easily described mathematically as due to the results of operation of a great number of small independent causes and most frequency distributions that represent the organic variability, in respect of some structural character—that is, the results of the measurements of some character in a large number of individuals, taken at random from a racial population, display this form of distribution. Most of the individual organisms included in such a distribution will be random fluctuants. It is very probable that any such fluctuant (or random variant, or variant by random fluctuation) will not have progeny, or progeny of progeny, that display the variation in the same degree. In other words, the random fluctuations are not inherited. This is a result of experience. The variations of numbers of vertebræ in, say, Greenland cod are random fluctuations.

Fluctuants by acquirement. Lastly, we consider those organic

variations that have been acquired by individual organisms in response to some need, or striving, experienced by them. Thus the thickened skin, or callus, that forms on parts of the hands of some artisans who hold tools, are acquired structural characters. We shall consider such variants by acquirement later in this chapter. It is sufficient to note here that such an individual variant does not usually have progeny that displays the same variation—that is, an acquired character is not usually inheritable. Perhaps it may be, but we shall further discuss the question later. It will be seen, from the discussion of this section, that, in a great number of individual organisms that belong to one local race there are some that display deviations, or variations from " the ordinary " in respect of any character that we measure. It is quite impossible to say, by mere inspection of these individuals, whether they are Mendelian variants, mutants, fluctuants at random, or fluctuants by acquirement. To say what is the nature of the individual variation breeding experiments, accompanied by inspection, are always necessary.

84*c*. Categories within the Local Race. We can now attempt to make categories that are finer than the local race. All such will, of course, conform to the definition of the local race —just as the local races of Greenlandic, Icelandic, Irish Sea, etc., cod, each has its own definition (depending on the number of vertebræ) but all conform to the specific definition of *Gadus callarias*. First we consider *Mendelian Categories* and we note that it is extremely improbable that these can occur in a wild population. In such individual organisms that display Mendelian inheritance there are characters that are reassorted at each act of sexual reproduction. There is an ensemble of characters, *E*, displayed by all the individuals and there are the " loose " " allelomorphic " Mendelian characters, *a* and *b*, *c* and *d*, *e* and *f*, etc. As the results of promiscuous matings these characters become reassorted in each generation so that we may have individuals displaying *E a c e*, *E a e f*, *E a d e*, *E a d f*, *E b c e*, *E b c f*, *E b d c*, *E b d f*, that is all the possible combinations of the Mendelian characters (that do not involve " lethal " results). This is what we should expect to find in a wild population—the random reassortments, or combinations of the characters, but no one category of individuals, all of them displaying *the same* combination of characters. We can make such a category by

controlled breedings and selection and, of course, it may occur, of itself, in nature but only with great improbability. Still we recognize the Mendelian category as a possible one, more or less probable if there is some agency in wild nature that corresponds to the agency represented by the experimentalist, or breeder in the laboratory or farm. By selection and inbreeding, then, we can make a category of organisms that have always the same characters (apart from fluctuations) from generation to generation —that " breed true."

It is also possible to establish " pure races " that are produced by asexual, or parthenogenetic reproduction. That is, it may be possible to select individuals from the local race that display some particular variation and then to reproduce these individuals asexually (for instance, by grafts, cuttings, etc., in the cases of plants). It follows, of course, that we must find inheritable variations, by trials. Then we rear a series of generations, from one ancestral organism, that differs somehow from other series of generations reared from other ancestral organisms. These are " pure races " produced, as in the cases of Mendelian categories, by selective breedings. They are what we may call *irreducible organic categories*. Their characters can be defined by some description, or diagnosis. We breed the individuals of the category among themselves and we observe that, from generation to generation, they " breed true," that is, in every progeny, or progeny of a progeny, the characters, as stated in the diagnosis, are reproduced. The diagnosis, or definition of the category will be, of course, wide enough to include those slight variations from " the ordinary " that we call fluctuations. That such fluctuating variations are " accidental " or non-essential to the diagnosis we prove by attempting to reproduce them. That is, we may select individuals from an irreducible category that display some exceptional value of a character (say great size of body) and then breed these individuals among themselves. We find, then, that the progeny, or the progeny of the progeny, always revert back to the original ordinary characters.

If then we study some irreducible category and find among its individuals some which do not conform to the definition, and have progeny which also do not conform to the definition, then we have observed transformism to occur. In order that such transformism may involve evolutionary change it is necessary

that it should be perpetuated, *in the conditions of wild nature*. That is, a new category of organisms should have appeared and some agency must have caused this new category to persist.

85. ON THE "CAUSES" OF MUTATIONS

Scientific method seems to oblige us to seek for the " causes," or antecedents, or conditions of appearance of mutations. We may best approach this problem by first considering more in detail what is meant by fluctuations and we are forced to investigate the matter from the purely physical side.

85*a*. THE MULTIPLE VALUES OF A CHARACTERISTIC. We take first, the most convenient model of a physical system, a small volume of gas at some constant volume, temperature and pressure. The individuals of the system are molecules and a characteristic of these individuals is their velocity. Each molecule moves with a certain speed until it collides with another molecule or with the walls of the vessel : then in general the speed changes. There will be a mean molecular velocity and a certain fraction of all the individuals will be moving with a speed that is a little less, or a little greater than this. Call the mean velocity v then the range $v \pm e$ will be that at which this fraction of all the molecules move. Above and below this range other molecules are moving, that is, there are fluctuations of velocity. There will also be fluctuations of pressure upon any small area of the wall of the container. We assume that all the molecules (say of hydrogen, H_2) are similar to each other in respect of mass, but there is really no reason for this assumption. All we know is the *mean* mass of a great number of hydrogen molecules and it is probable (or it is just as reasonable to assume) that the mass of the individual molecules fluctuates about a certain mean value.

What we have said applies also to any other measurable physical characteristic as observed in inorganic individuals—that is electrons, atoms, molecules, crystals, colloidal particles, etc. The characteristic (mass, speed, form, etc.) has a mean value and there are fluctuations in the individuals from this mean value. We do not easily observe such fluctuations in the cases of atoms and molecules since these are so small that what we always infer is a statistical result—the mean of a great number of individual effects. Still we can conclude that every physical result has

multiple values ; that one range of values, $v \pm e$, is more probable than any other one ; that there are other similar ranges of values that are less probable and that the further removed from the mean is any range of values the less probable it is. This is exactly what we find in the frequency distribution of any one organic character in a number of organisms. We tend to think of some privileged value of the character—a value that " ought to " exist, but what we really observe in nature are multiple values that are more or less probable.

85*b*. Organic Fluctuations and the Environment. Even in an irreducible category of organisms there are such fluctuations. We may, for instance, establish a " pure race " of bean plants, all of them being derived from (or are the progeny of) a single bean and being perpetuated asexually. Even in a single pod borne by such a plant the individual beans will differ in weight, and we are inclined to see that these individual variations are due to the environmental conditions : slight differences in position, in conditions of nutrition, etc. But it is easy to see that the environmental influences only condition the range of the fluctuations. Thus we may incubate a number of eggs of, say, a pelagic fish and observe that the mean period of incubation (that is, the time that elapses between fertilization and hatching) is so many hours but that this period varies considerably in individual eggs. If now we change the temperature of the sea-water in which the eggs incubate we shall see that the mean period of incubation is changed (being increased for a reduction of temperature and *vice versa*). But there will still be a somewhat similar range of variation in the times at which the individual egg hatches out in the changed environment and we conclude that the existence of fluctuations is independent of these latter changes—which only influence the position of the central point about which the variable character fluctuates.

What we observe in such cases as the growth of the beans, or the embryogenies of the fish eggs are instances of a repetitional developmental process—something roughly analogous to the series of operations by which a minting machine strikes out coins intended to be of precisely the same forms and weights (though it is only by analogy that we think of the " intention " of the developmental process, or organization). But it is clear that the products of the minting machine are not precisely alike, because in the process

there are included a multitude of small, independent, contributory causes which lead to a certain statistical result, but also to a number of "accidental" variations from that result. The developmental agency manifests itself (just as the ideal minting machine does) in the assemblings of material-energetic things and the fluctuations are in these assemblings of chemical substances and energy-transformations.

85*c*. Mutations Regarded as very Improbable Fluctuations. Again we approach this problem from the purely physical view-point. Let there be a physical-chemical system of OH_2 and CO_2 molecules with light radiation impinging on these individuals. They are "energized," that is, they move with a certain mean velocity, but there will be some molecules that move with velocities much greater than this mean. Let the frequency of the incident radiation increase and it may happen that a few of the CO_2 and OH_2 molecules become highly energized so that they move with greatly increased velocities, or their internal (electronic) energies become greatly increased. We may regard such "super-energized" molecules as very exceptional, or improbable fluctuants. They may, in this highly energized condition, then combine to form formaldehyde—which, in a way, may be thought about as a chemical mutation. Again the molecules of yellow phosphorus have, in that phase, mean energy-values and there are in the multitude of molecules that make up a small mass of the substance, some that fluctuate much above this mean in energy-value. Let the phosphorus be heated out of contact with oxygen to a certain temperature and these exceptional fluctuants greatly increase in number and in energy. The phosphorus then undergoes transformation into its red, allotropic modification—that is, a chemical mutation has been effected.

Something analogous to this occurs when mutations are "induced" in organisms. Thus the eggs and larvæ of some animals may develop in unusual ways when the pregnant parents are exposed to temperatures, or other physical conditions, that are very exceptional but are not so exceptional as to kill the animals. Drosophila, which is bred, for experimental purposes, in highly artificial conditions has been fertile in displaying mutations. Certain goldfishes reared in small aquaria, in rather stagnant water, give curious mutations. Generally domesticated plants and animals are bred and reared in conditions differing

greatly from those under which their wild progenitors lived. In short, there is some evidence that marked changes in the environmental conditions—which changes do not render organisms "unhealthy," or inhibit their reproductive powers—may affect the gonads and the developmental processes. It is not known whether the germ-cells are thus affected directly, or *via* the general bodily tissues that environ them. It was inconceivable to Weismann that the germ-plasm (that is, the chromosomal material of the germ-cells) could so be affected, but there seems now to be no doubt that this may happen. Now such reaction between the germ-cells and the environment is something analogous to the purely physical processes alluded to above.

But a mutation is a change in some character of an organism which is also displayed by the progeny, and the progeny of the progeny, etc., of that organism : it is said to be an inheritable change. Therefore the developmental organization has been changed. We note, in passing, a fact of much significance, that the mutation "Mendelizes," that is, it may appear in some of the progeny, or grand-progeny, etc., but not in others. When it does not appear in the progeny, but reappears in the grand-progeny it is said to be "recessive"—it is still there, in a way, but is not manifested. This is the fact of observation which must clearly be distinguished from the statements of the hypothesis of genes. We have already noted it in saying that the agencies which lead to the appearances of the mutational character are "loosely attached" to the developmental organization. Now it is clear that the latter is not a physico-chemical system, or, at least, we have seen what are the enormous difficulties in believing it to be such. Therefore it is not easy to see how an agency which is best conceived as psychological in nature can react to some physico-chemical change in the environment in the way that, say, yellow phosphorus reacts when it changes to the red, allotropic form. We can make analogies : thus builders accustomed to work with stone are compelled to work with steel and concrete so that the designs of buildings have undergone "mutations." But obviously the analogy is indicative at the best and it is suspect, to many minds, because it is "anthropomorphic." Clearly the problem of the "origin of mutations" is not yet satisfactorily dealt with. Perhaps it is a pseudo-problem that arises from our difficulty in postulating changes to happen without those changes

having antecedents or "causes." Perhaps the occurrence of real "uncaused" novelties in the racial histories of organisms may simply have to be accepted.

86. *ON HYPOTHESES OF TRANSFORMISM: I. NATURAL SELECTION*

We have not considered those variations that we have called "acquirements" because it will be more convenient to deal with them when we discuss "Neo-Lamarckism." Meanwhile it has to be emphasized that the occurrence of novelties of character is the starting-point in any hypothesis of transformism that involves selection. The occurrence of a novelty, or a mutation (as we may agree to say), is not, in itself a transformist process, for the latter must include the establishment of an enduring category of organisms. A mutation is a change which may occur in one, or in a few individuals of a population, but some process must go on whereby the novelty of character becomes widespread in the population so that a new "breed," "race" or species comes into existence. Further, the new category must, in some way, become physiologically isolated from other ones originally associated with it so that it will tend, at all events, not to interbreed with those other categories.

86*a*. The Modes of Origins of Races of Domesticated Plants and Animals are not necessarily those of New Categories of Wild Organisms. This we can see when we consider how such domesticated races originate and are maintained. Breeders, farmers and agriculturists observe the occurrence of some noticeable "sport" or mutation, or they observe that some individual organisms, rather than others, have desirable qualities: fruits may be larger or more succulent; the grains of some cereals may make better bread-stuffs; milch cows may give a better yield, etc., or the sport may be desirable merely by its appearance (as in fancy pigeons, some dogs, some cats, etc.). In any case there is the motive of perpetuating the novelty in a race, or breed, and so the organisms that display it are inbred, or are self-fertilized, or reproduced asexually if they are plants. That is to say, the breeder exercises control over the reproduction of the individuals that he wishes to perpetuate by selecting, for interbreeding, those that have the desired

qualities, by controlled matings, intensive inbreeding and so on. It is unfortunate that there are few good accounts, by practical breeders, of all the trials, successes and failures by which a " breed " become established, but the records of experimental operations point clearly to the methods involved. These, in brief, mean selection and controlled matings. Now if we are to extend the experiences of the experimentalists and practical breeders, so as to explain the processes of natural transformism it is necessary that we insert, in wild nature, some process of controls that operate in analogous ways to those practised under artificial conditions.

86*b*. THE RESULTS OF MENDELISM DO NOT AFFORD AN EXPLANATION OF NATURAL TRANSFORMISM. Even when we accept the main results of Mendelian research there is something wanting. Mutations occur. These novelties in bodily character are paralleled by changes in the developmental organizations of the organisms that display them and we may say, meanwhile, that new developmental factors come into existence. The new factors are not integrated into the developmental ensemble so that they are " loose " and may assort, reassort, link, etc., at each maturation of the germ-cells, or at each conjugation of the gametes. This means that, with the restrictions imposed by " linkages," the organisms that result from the sexual matings may display many combinations of the " loose " characters. It is also plain that, by selection of the individuals that are to be mated categories may become established and it is possible that (within the restrictions suggested above) categories of organisms displaying any desired combination of loose characters (that is, characters capable of assortment and reassortment) may be established. Further, *under the conditions of continued control*, such categories may be maintained.

But in wild nature the conditions of controlled matings do not exist (or we insert those conditions, *by hypothesis* into wild nature). There may be " instinctive antipathies " between the individuals belonging to different species, whereby they do not attempt to mate, but we do not know of such antipathies between individuals that differ only in respect of Mendelian characters. We may, therefore, conclude that, in wild conditions there is complete promiscuity of mating between Mendelian variants and so it follows that there are no Mendelian categories such as may be established and maintained by human artificial controls. Or, at

least, such categories may only occur with a high degree of improbability (which ought to be capable of calculation.) If, then, we make use of Mendelian results in the attempt to frame a hypothesis of natural transformism we must again insert some process *that is anti-random* into wild nature.

86*c*. The Hypothesis of Natural Selection. As formulated by Darwin and Wallace the hypothesis is simple and very logical. Briefly, the steps are as follows: organisms tend to multiply to an indefinite extent, but their food-supply, shelter, and even the space available to them are all strictly limited. Therefore far more individuals come into existence, as eggs and embryos, and survive for a short period as larvæ, or juveniles, than can possibly continue to exist long enough to reproduce again.

There must, therefore, be competition among the organisms of a race, or between those organisms and the individuals of other races, for the limited food and shelter that nature provides. This is "the struggle for existence." Now organic variability (of whatever kind it may be) becomes a factor in the struggle. There must be variants in the race-population that are larger, more powerful, more speedy, with greater acuity of sense, with mentalities that are more alert, etc. These variations must confer advantage upon the animals that display them so that they will be more successful in the struggle. Conversely there will be individuals that display variations that are disadvantageous to them. It is clear that, on the average, the variants that have bodily advantages, in this way, will live longer and will reproduce more often than those other individuals that have bodily disabilities. Thus the "fittest" will tend to survive, while the "unfit" will tend to be eliminated in the struggle for existence. The conclusion, so far, is obvious and is valid whatever be the nature of the variations that are of advantage, or are disabilities —whether these variations are mutations that Mendelize, or are fluctuations, or are acquirements.

The next step in the argument is the questionable one. It was assumed by Darwin, Wallace and their followers that all the variations that naturalists can observe in wild organisms are "inheritable," that is, that just these variations will reappear in the progeny of the organisms in which we observe them. Let us admit, for the moment, that this is true: then it can be shown that transformism must occur. Let the graph *A*, Fig. 35, repre-

sent the frequency distribution of some variable character in a population of the same race: Let this character be such that if it varies above the average it will confer advantage on the variant.

The mean value of the variable character is exhibited by the group *a*. The groups to the right of *a* display the variable character in higher degree than do those at *a*. Conversely the groups to the left of *a* display the character to a lesser degree. All the groups to the right of *a*, say those at *b*, have therefore some advantage over the *a*'s in the conditions of the struggle for existence—they are the "fitter." And therefore more of the *b*'s

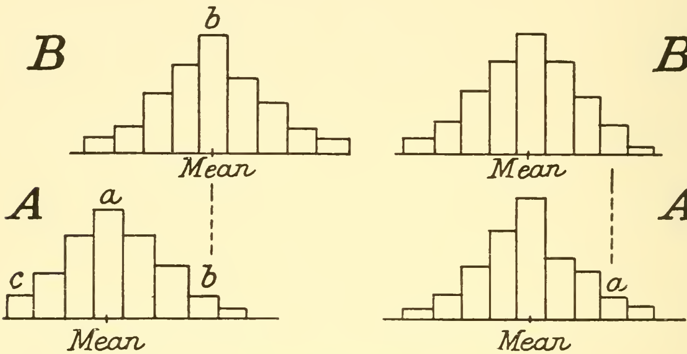


FIG. 35.—DIAGRAM SHOWING REGRESSION.

will survive and reproduce than their numerical proportions in the distribution would suggest. Conversely less of the variants to the left of *a*, say the *c*'s will survive and reproduce.

But the *b*'s have displayed a variation that is advantageous and which we assume to be hereditary. Therefore the progeny of all the *b's* that have reproduced will also display this variation. Let us, for simplicity, take the extreme case: the new frequency-distribution of the value of the variable character is represented by the graph *B* and this shows that the advantageous character, which was exceptional in its occurrence in *A*, is now at the mean in *B*. That is, the exceptional variants in *A* are now the ordinary individuals of *B*. Clearly transformism has begun and will continue, for the same process of advantageous variability, and the transmission of this to another generation, will begin anew from the exceptional variants of *B*. Thus a new category of

organisms (the B-one), differing from the A-category in that some advantageous character has changed so that it becomes more advantageous, will have arisen. Now, as a rule, several characters will vary in the same ways. Also an actual novelty of character may have originated in one, or a few variants in A and since this novelty, or mutation, is an advantageous one it will be largely increased in frequency in the B's (or progeny of the A's) because the variants in A were enabled to survive and reproduce often. Clearly the results of these processes will be that a new category of organisms to which the original definition does not apply will have evolved. And we may reverse the whole argument, as stated above : assuming, instead of advantageous variations, some that are disabilities to the organisms that display them. Then it is easy to see that transformism will occur, but now the variants in question will fail to survive, will not reproduce, or will survive in smaller proportions and so there will be fewer progeny. In the long run such disabled variants will tend to be eliminated from the race.

The question arises now—are the variations that we observe in a naturally occurring population inheritable ? Experience has proved that, in general, they are fluctuations and are not inherited. If we select from a stock of wild animals some individuals that are, say, larger than the mean—those at a in the graph A' of Fig. 35 for instance, and if we now breed from them the progeny that we obtain will tend to *regress* towards the mean of A'.

Thus the children of exceptionally tall (human) parents will tend to be taller than the mean of the whole population, but they will not be so tall as their parents. And even when inbreeding is practised this regression towards the mean value of stature in the population will occur. Clearly the ordinary variations that we see in a race-population are not, in the long run, inheritable ones. A variant taken at random *may* display a variation that is inheritable, but experience has shown that such variants occur only exceptionally. And the result is even more clear when we experiment upon a " pure race," say the classical beans. If we rear plants from the heaviest beans taken from a plant of such a pure race the mean weight of the beans produced by these daughter-plants will be just the same as the mean weight of the beans produced by the parent-plants.

Therefore, the natural-selection hypothesis is *logically* sound and it will be actually sound if the condition—that a certain proportion of the individuals of the race we experiment upon display inheritable variations—is realized *in wild nature*. We must now appeal to the facts of observation. What is " a certain proportion "? This means the analysis of the nature of the variations—whether Mendelian, mutational, fluctuating variations, or acquirements. Is the proportion of inheritable variations great enough to enable such a process of transformism as we have suggested above to go on at such a rate as to explain the evolutionary career? Further (as Bergson urged in an argument that still retains its force), the transformist process, or the selection hypothesis, will usually include combinations of favourable variations. What are the probabilities of such combinations occurring *at random*. In most cases these probabilities will be small ones, so that the rate at which transformism proceeds will be further lessened. Clearly the natural-selection hypothesis is logically strong; clearly it involves only randomness in respect of the occurrence and combining of variations, and is so far satisfactory (to many minds) in that it dispenses with " purpose " in wild nature. But it is still necessary that the hypothesis should be verified by statistical observations made upon naturally occurring populations and such observations—upon an adequate scale —do not exist.

Two problems more press for treatment. (1) The origin of mutations (which we have already dealt with and (2) the meaning of the " selection " idea. What is it that " selects " in natural conditions. Plainly it is the urge to live and reproduce. It is rather " auto-selection " that we mean instead of selection " by nature." If the organism is fit it will live and reproduce and so its " breed " will persist, or accumulate. If the organism is not fit it will be exposed to greater risks. The idea of " auto-elimination " is perhaps more clear than that of auto-selection. In Mendelian variants we see, most plainly, the organisms exposed to risks. The combinations of characters studied in Mendelism are mostly such as are disabilities (thus the more obvious ones in man, hæmophilia, night-blindness, colour-blindness, the mutilations of extra digits, stumpy-fingers, etc.). If such combinations of characters occur at random, in the cases of natural populations they must afford the " materials for elimination."

And it is interesting to note the importance, in this connection, of " lethal factors " in Mendelian studies. A lethal factor appears to be some unfavourable combination of characters, or " a double dose " of some factor—in any case the organism that has a lethal factor dies in the course of its development.

87. *ON HYPOTHESES OF TRANSFORMISM: II. NEO-LAMARCKISM*

In such hypotheses is implied the notion that organisms change their habits, functioning and structure by actual, inward efforts or strivings and that they may have progeny that inherit the changes brought about by these parental efforts and strivings. Thus the changes in habits, functioning and structure *acquired* or made personally by the parents produce changes in their developmental organizations and so transformism occurs.

87*a*. ACQUIREMENTS. Among the variations from " the ordinary " observed in a racial, wild population are those that are called acquirements. Individuals displaying such are called " variants by acquirement." Quite provisionally we define an acquirement as some change of habits, functioning or character that occurs in an individual organism after (so far as we know) all the inherited characters have been fully developed. (But it is, of course, never certain that any change that occurs after development appears to have been completed is not simply an example of exceptionally late development.) Acquirements may be roughtly classified as (1) *adaptations* and (2) *mutilations*.

Adaptations. Typical examples of such changes of structure, functioning and behaviour are :

The whitening of the coats of some polar animals when the winter conditions develop ; the thickening of the furs of cats kept in cold-storage warehouses ; the thickened skin pads on the hands of artisans who hold and use tools in particular ways.

Excessive secretion from the skin (in men) during hot weather ; increased secretion from the kidneys at the onset of cold weather ;

All animal training ; the opening of a latch by a dog ; recognition of the dinner bell by a dog ; expediency in traversing labyrinths, etc., by crabs, rats, etc. ;

Swimming by men and women ; making and using tools ; the

fabrication of nests and burrows by many animals ; building houses, ships, etc., by man ; the operations of artisans, musicians, surgeons etc. ;

The increase in size and efficiency of muscles that are much used (as by blacksmiths, pianists, etc.) ; increased heart-power by athletes ; repairs of bodily injuries carried out by doctors ; plastic surgery ;

Increased physique and better health of children due to improved food, sanitation, clothing, etc. ;

All education and art.

These examples illustrate adaptations and they will be sufficient to indicate what are the general characteristics of such changes. It is to be noted that few of them apply to organisms living in wild nature and that they mostly refer to cases where some kind of human control or interference has occurred. In the present phase of the investigation of transformism this experimental method is necessary and for a time the methods of the laboratory must be applied. Nevertheless, it must be noted that it is the evolutionary career which we are studying ; that transformism has occurred in the past independently of human interference and control and that whatever explanation we make as to the details of the process must be based on naturalistic observations—those of the scientific man who is solely a *spectator* and not an experimentalist. Meanwhile, of course, the laboratory methods are fashionable, and indeed indispensable.

The examples show, however, that an adaptation (1) is not merely a passive change undergone by an organism. We must not think of an organic adaptation as being illustrated (as the term suggests) by, say, melted typemetal adapting itself to the form of its environment, that is, to the mould into which it is poured. (2) It is *an active response* on the part of the organism to something in its natural surroundings : the muscle that is used to a higher degree than the ordinary, as in the case of the athlete's heart, increases in size and efficiency, or a part of the epidermis may thicken so as to resist the increased friction which exceptional activity sets up. (3) There is a specialization of some kind in the relation between the animal and some things in its environment which have particular significance. (4) This relation of specialization is made by the animal itself.

Mutilations. These are acquirements—changes of structure,

functioning and habits that are *suffered* by the organism. They are (1) *Diseases*, that is, disorders of functioning due to intoxications, bacterial or parasitic infections ; deficiency-conditions due to some defect in nutrition (as, for instance, thyroid-deficiency, vitamin-deficiency) and so on. (Here, of course, we exclude disease that may possibly be " transmitted by heredity," as in gout, rheumatism, possibly cancer and epilepsy.) There are also disorders of growth, etc. (2) Mutilations may be *traumatic* in nature, that is, the results of " accidents," say, losses of bodily parts, such as limbs. (3) They may be the results of some *operative interferences* carried out experimentally : castration, circumcision ; the removal of some bodily part, as in the docking of the tails of some dogs ; section of a nerve, blinding ; interference with an embryonic process, etc. In extreme cases mutilations are fatal injuries, as in the results of accidents, many experimental conditions, or diseases that lead to death. But many prominent mutilations are consistent with normal, reproductive life, as in the human conditions of partial or total blindness, the excision of bodily parts, such as a kidney, the loss of much lung tissue by tuberculosis, etc. In experimental conditions such mutilations are deliberately caused and are intended to have some bearing on the general problem of the inheritability of mutilations. (Weismann's experiments on cutting off the tails of rats, for instance.) It is such mutilations as are compatible with continued reproductive life that we consider later on. In general, mutilations must be regarded as disabilities. In the cases of men and women, living in civilized communities, this may not be the case. Nor in the cases of experimental animals, or those that are domesticated or are living under laboratory conditions need a mutilation be a disability. But in wild nature, and under the stress of severe competition, all such mutilations as we have indicated, or all malformations, or all results of accident or disease must be regarded as, to some extent, disabilities. We emphasize the contrast between them and adaptations—which tend, in general, to the increased power, on the part of the organism, over some part of its natural environment.

87*b*. Transformism by Acquirement. Just as in the cases of fluctuations, mutations and combinations of Mendelian characters, acquirements may be the materials for selection. It cannot be doubted that a positive adaptation of behaviour,

functioning or structure confers advantage upon an organism so that it will tend to live longer and reproduce more often than do organisms of the same race that have not made the adaptation. And conversely a mutilation must expose the organism to some disability so that it will not live so long, nor reproduce so often as do those that are not so mutilated. But all this need not lead to transformism. In order that this may occur it would be necessary that the adaptation, say, should not only be something that is novel but that it should also be such a change that will necessarily occur in the progeny of the organisms in which it first appears. Now leaving, for the moment, this question of the inheritability of acquirements we may conveniently discuss the *logical* argument for Lamarckian transformism.

Urges, needs and desires in organic behaviour. We have seen (Sections 46 and 47) that the animal so behaves as to maintain itself in a condition of normality. It so acts as to maintain its own individual existence and to reproduce. If the environmental conditions change, it so modifies its behaviour as to establish new relations with regard to the things outside itself such that the state of normality may be restored. It has still its urges to live and reproduce and these must be satisfied if it is to retain its normality. Its urge to grow and reproduce is indefinitely great and is limited only by the opportunities that wild nature affords for nutrition, shelter, and space for the indefinite distribution of its progeny. Therefore by " normality " we must also understand the potential increase of its race to an indefinite extent. So even should the environment remain the same the organism and its progeny must continually endeavour to find in it new opportunities for nutrition, defence against enemies or unfavourable conditions, and for reproduction.

If these urges are not satisfied the organism must experience needs and desires. It does not follow that such needs are " felt " : they may be experienced unconsciously as lack of normality. There is simply *dissatisfaction*, whether the lack is consciously experienced, as it doubtless is so experienced in ourselves and many other animals, or whether it unconsciously affects behaviour. We experience dissatisfaction, or lack of normality, when we are hungry, but even when we cannot attribute the unconscious feeling of hunger to an organism there must, nevertheless, be an urge to renewed assimilation.

The dissatisfaction of an urge leads to modification of behaviour, via the method of trial and error. Clearly any behaviouristic process has a pattern, but the pattern varies. Further, the mechanism of limbs, muscles, nerves, nervous centres and sense-organs is capable of acting in a variety of patterns (walking, running, leaping, swimming in mammals). The pattern is surrounded by a fringe of random activities. This degree of randomness is the opportunity for the formation of new patterns, or variants of the existing one. Some such variant is tried and is found not to satisfy the urge, is tried again and is found to give satisfaction. Thus a new habit is formed, is found to be successful and is retained by conscious or unconscious memory, or motor habit, or by the survival of a neurone-path from several that have been tried.

The new habit reacts on functioning and structure. Or rather variants of functioning and structure express the new habit. Speaking has led to the establishment of a unilateral cerebral speech-centre ; right-handedness has led to a strong development of muscles and muscle-scars on the right shoulder and arm ; increased bodily exercise leads to more vigorous action of the heart and so to greater development of the heart-muscle ; and so on. Conversely the disuse of bodily parts leads to their reductions in activity and size, and perhaps to atrophy or disappearance. Thus it is just as " reasonable " to argue *a priori* that blindness of animals that live habitually in the dark follows from the disuse of eyes as to argue that such blindness is the result of natural selection. Or it is equally plausible to conclude that wingless insects on oceanic islands have come into existence from continued disuse of the wings as to conclude that wingless insects in these habitats are the results of the elimination of winged insects (by reason of the latter being blown out to sea).

Acquired processes become habitual ones in individuals. There is no reason to doubt this conclusion since ordinary observation and deliberated experiments demonstrate it. In some animals habits are easily acquired, both by training and spontaneously, and such habits persist. In ourselves habits are continually being " formed," while skilled activities involving the muscle-brain-sensory system are acquired as the results of imitation and training. Such processes are carried out at first to the accompaniment of acute consciousness and they may be clumsily effected. But what

we positively know about the nervous system suggests that a complex motor habit is made possible by some structural changes involving cerebral tracts and groups of synaptic connections. Apparently when these neurone-patterns have been established the activity becomes an automatic one, is performed with facility and, it may be, with an entire absence of consciousness of its performance—that is, the acquired activity has become a habitual one. The above statements apply particularly to neuro-muscular activities, but they may be extended so as to include what is called organic functioning. Thus a conditioned reflex which involves the secretion of saliva may be regarded as a glandular habit. Acquirements, whether made spontaneously or as the results of training, thus may become habits in the individual animals that make them.

Habits become instinctive activities and thus transformism is effected. This is, of course, the doubtful step in the argument. The acquirement, made spontaneously, or by imitation, or by training, must be " transmitted by heredity " so that it occurs again (without being " evoked " by imitation or training, and in such a way as to suggest that it is not " spontaneous " in the sense used above) in the progeny of the animal in which it first appeared. That is, the habit, which depended on random fluctuations of the behaviouristic mechanisms, now involves the developmental organization so that the ability to do something, and the corresponding changes of structure, are " congenital," " inborn," or have become instincts and morphological changes. It is difficult to resist coming to such a conclusion, which seems to be the natural one. It is difficult to avoid thinking that the continual repetition of an acquired habit, from generation to generation, will, by and by, come to affect the developmental organization so that the activity will be displayed " instinctively," or without being acquired. Such views have always been held both by laymen and naturalists. (" The fathers have eaten sour grapes and the teeth of the children are set on edge.") Much in human affairs suggests that acquired activities (mental, or motor, or functional) tend to become transmitted by heredity. For instance, the phenomena of immunity to some diseases that follows upon prophylaxis seems to point to such a conclusion. It has been said to be " inconceivable " that the acquirement of some activity, or morphological change, can affect the " germ-plasm " so that the acquirement

becomes a hereditary one, but so far from being inconceivable was such a conclusion that, until the time of Weismann, it was commonly held. In pure natural history the transmission of acquirements seems to be the most obvious way of explaining many cases of transformism—the adoption of a gasteropod shell as a shelter by the Hermit-crab, for instance. Of course so great is the generality of the logic of natural selection that such cases are equally well explained (logically) by the latter hypothesis.

If we admit that acquirements may be slowly transmitted by heredity it becomes easy to formulate the corresponding hypothesis of transformism. The increased use of some bodily part reacts on structure so that bodily proportions become changed—in such a way we might explain (logically) the gradual increase in size and efficiency of the 3rd digit in the feet of the Tertiary horses ; the practical elimination of the other digits and so the evolution of the Equidæ. Or the occasional swimming of some terrestrial mammals may be thought about as becoming a habit, reacquired by imitation, generation after generation and reacting on structure until the forms of the limbs became so changed as to lead to the evolution of flippers adapted for locomotion in water. Obviously the logical argument is a very plausible one.

87*c*. THE EVIDENCE FOR LAMARCKISM. Some things are demonstrable. (1) The general validity of the method of trial and error : observation of organisms living in the wild and laboratory experiments prove this. (2) The passage of an individually acquired activity into a habitual one. (3) The automatism of habit and the performance of learned, skilled activities without consciousness. (4) The effects of use and disuse of organs and bodily parts in producing structural and functional changes. There remains the all-important demonstration—that such individual acquirements may reappear, not as renewed acquirements but as hereditary qualities, in the progeny.

Here we must make appeal to facts. And it has to be admitted at once that the appeal is inconclusive. Logically the hypothesis of natural selection is sound, but we find it impossible now to show that the naturally occurring variations by fluctuation on which Darwin and Wallace built their case are changes that reappear in the progeny—or are transmitted by heredity. Nor can we show that mutations occur so frequently as to constitute such an abundant material for selection that transformism must result.

We have seen that mutations appear ; can be loosely incorporated in the developmental organization ; can be reassorted in each hybridization that occurs from sexual mating so that we can have combinations of characters, or transformism. But all this occurs under human control and we must extend the results to wild nature before we can attempt to explain evolution. Here again the appeal to natural facts—to the populations living in the wild—fails. We know that races of organisms have been domesticated, reared, inbred, etc., so that transformism undoubtedly occurs under artificial conditions, but this is not enough : we have to show that there are analogous processes operative in wild nature and this has not been demonstrated. So, with regard to Lamarckian transformism, we have to show that acquirements made by, or experienced by individual organisms can change the developmental organization so that these acquirements become hereditary changes.

All that can be said is that the meagre evidence that we have points to that conclusion. There is, of course, much experimental " proof " that this is not the case—proof that hardly applies to our problem. Undoubtedly it has been most difficult, and perhaps impossible, to show that experimentally produced mutilations become hereditary. For instances, the tails of many generations of rats and terrier dogs have been amputated but still the descendants of many generations of such mutilated animals are quite normal and do not exhibit the mutilation. We ought to be very much surprised if we did obtain such a transmission of a mutilation, for we have only to reflect that all organisms in wild nature are continually exposed to innumerable risks and suffer from the results of accidents. We know that, even before reproductive vigour has failed animals have " aged " and have acquired disabilities—which nevertheless do not reappear in their progeny. Nothing is more surprising, upon due reflection, than that experimental mutilations should have been practised upon animals with the expectation that those changes would reappear in the progeny. It is even more surprising that the failure to obtain such results should have been held to be a demonstration that Lamarckian transformism did not occur.

It is different with regard to adaptations. It seems " reasonable " to expect that slight, advantageous changes, made generation after generation, would eventually affect the developmental

organization. Such observations, and experiments bearing upon the same problem, have been made again and again and with apparent success. Yet there has been constant controversy as to what these experiments and observations demonstrate. Without doubt it has been fashionable in biological investigation, since the time of Weismann and all through the period of modern genetical studies, to distrust such views as were almost dogmatically held before the time of Weismann. And the experiments and observations expected to demonstrate Lamarckianism are laborious and difficult to verify and so some doubt always attaches to their results. But what big experiments have been made do seem to point strongly to the conclusion that small adaptations, or even apparently indifferent bodily changes made throughout many generations, at last become changes included in the developmental organization. That means that individual acquirements become congenital changes, or there is transformism.

Clearly we have, at present, no generally accepted hypothesis of transformism. (1) Contemporary investigation is almost entirely experimental and the tendency is to apply its results to the study of the evolutionary career. Certainly we can actually *observe* transformism in progress in all cases where plants and animals are domesticated and bred as "stocks" that have utilitarian value. Certainly every Mendelian experiment demonstrates transformism. But it would be foolish to argue that results obtained by human, experimental control can be extended to the past, pre-human phase of life on the earth *unless we insert into that past some agency comparable in effect with human, experimental control.* And even then all Mendelian results that are applicable to the study of the evolutionary process must postulate the occurrence of mutations, that is, real novelties of character, and this formidable problem is untouched by any contemporary experimental work. (2) The Natural-Selection hypothesis, logically powerful as it is, nevertheless depends on some estimate as to the existence, in wild nature, of inheritable novelties of character, or mutations, that may be the material for selection. Therefore, to render that hypothesis verifiable we must have some notions as to the numerical values of occurrence of these mutations, and some fairly precise notions as to the rate at which evolutionary changes have proceeded. And again we merely take for granted the occurrences of these mutations—without any notion as to how

they occur ; this, of course, is the real problem. (3) Finally, we have the almost obvious hypothesis of bodily changes occurring as the expressions of needs and desires, and then the gradual modification of the developmental organization by these bodily, individually acquired changes. We easily see, from the literature, that experimental evidence in favour of such a hypothesis exists but is, at the best, inconclusive and not generally accepted. But even if such evidence were beyond question we have still to extend it to wild nature and show that something happens there comparable with what our experiments do. So we are again in the phase of biology that preceded the work of Darwin. Experiment suggests conclusions that can only be applied to the study of the evolutionary process after far more work of the purely natural history kind than is now being attempted. It is the study of wild nature, without experiment, that must be the next big step forward.

CHAPTER IX

THE EVOLUTIONARY CAREER

I. EVOLUTION IN GENERAL

(*a*) Let some physical system undergo repeated changes in such a way that these changes have, on the average, some particular direction, or tendency: we shall say, then, that the system "evolves."

(*b*) And since the changes may occur along different directions, or exhibit different tendencies, it is plain that systems may "evolve" differently.

(*c*) Let a physical system undergo repeated changes that have, on the average, no tendency, or direction: then the system does not "evolve." (Presently we shall consider more fully what is to be meant by the word "evolve.")

Familiar and trivial examples of these statements are afforded by study of the card games called "Patience" ones. The pack of cards is shuffled (or mixed up, so that inspection shows no particular order) and then it is distributed according to certain rules, or conventions. As the distribution (or the repeated changes of the card-system) proceeds the cards come to exhibit a particular arrangement—which may be said to "evolve." And there are many different kinds of "Patience" games so that the same system (or pack of cards) may be made to "evolve" in as many different ways, as there are sets of rules, or conventions.

Let a pack of cards arranged as they "come out" in a successful "Patience" game be repeatedly shuffled. As the shuffling proceeds the particular arrangement disappears. Then, as shuffling still proceeds there will be a very great number of arrangements, but any one of these will occur as often as any other one and there will be no tendency in these arrangements. While the particular arrangement brought about in the successful game is disappearing we may say that there is an "evolution" —in a different sense (from "order" to disorder)—from that of

the evolution that occurs when the arrangement of a successful "Patience" sequence is being built up. When this arrangement disappears there is no longer an evolution.

88. *ON EVOLUTION AND PROBABILITY*

A pack of cards may be arranged in $\underline{|52}$ different ways ($\underline{|52}$ means the product $52 \times 51 \times 50 \times \ldots \times 3 \times 2 \times 1$). But there may only be one way in which 52 cards can be arranged as the result of a successful Patience-game. Let us suppose that the cards are dealt "at random," that is, without any conventions. (By "blind chance.") It is still possible that they may be so dealt as to exhibit, "by chance," a particular Patience-sequence. Obviously the probability that this may happen is 1 in $\underline{|52}$, which is a very small chance.

Nevertheless, the Patience-player, by dealing the cards according to certain conventions, may obtain the particular sequence, say once in every ten trials. The probability consequent upon dealing according to the conventions is now one in ten, which is very great compared with the probability of obtaining the sequence as the result of "blind chance." But, again, the player may quite easily and deliberately free himself from any convention and select and arrange the cards, one by one, and from a shuffled pack, and cause the sequence to occur *once in* every trial. The probability is then one in one.

Thus there are sequences, or particular orders of things, or special arrangements, which occur, at random (or by "blind chance"), very infrequently, or with a very small degree of probability. On the other hand, if "blind chance" is replaced by *deliberated selection* the sequence, or special arrangement, may be made to occur with a very much greater degree of probability.

Plainly there ought to be two *contrasted* evolutionary processes: (1) That in which some particular order, or arrangement of the elements of a physical system, results from changes in a prior phase which did not exhibit the particular order, or arrangement. (2) That in which a particular order, or arrangement, disappears as the results of the changes that occur in the system.

We must now show that the process (1) "models" organic evolution and that (2) "models" inorganic and cosmic evolution. In the years following the general acceptance of Darwin's hypo-

thesis of natural selection it was generally held that there was one process of universal evolution and that stellar, planetary, geological and organic evolutionary processes were all phases in one general process. We can now easily see that this view is unsound and that the process of organic evolution exhibits a tendency which is the opposite to that of stellar, planetary and geological evolution.

89. *ON THE TENDENCY IN COSMIC EVOLUTION*

On the older views the stars and planets were regarded as very hot bodies that were cooling, or had cooled down to the temperature of cosmic space. This is true, but it is not the whole truth. The consequence of the views was this : there were concentrations of energy in the universe and these were the stars. If we were to " sample " the universe by taking blocks of space of, say, one billion of miles in volume there would be a certain, rather small probability that any such block taken at random would contain a concentration of energy—that is, a cooling, but hot star. On the other hand, so far apart from each other are the stars that the probability that our sampled volume would *not* contain a star would be much greater.

As the stars cool their energy is radiated away as heat (low-frequency radiation) and this energy travels in all directions throughout interstellar space. The more the hot stars cool down the less energy they " contain," but the more energy is " contained " in the interstellar space. Finally (when each star gives off just as much energy, as heat, as it receives from the heat given off by all other stars), all universal stellar and interstellar space will be at the same temperature. Therefore, while cooling is going on, energy becomes more and more uniformly distributed and the probability that random sampling of cosmic space would give equal energy-contents would become maximal.

The recent cosmogony does not affect this conclusion. First it was shown that hot stars, like our sun, and cold bodies, like the earth, emit energy that comes from the radio-active disintegrations of atoms like those of uranium. But however protracted such a source of energy must be, it must ultimately fail and these emissions of high-frequency radiation ultimately degenerate into low-frequency radiation, or heat. And the latter tends to become uniformly diffused throughout interstellar space, as before.

Then it has been held, in quite recent years, that the energy that is emitted by a hot star may come from the " annihilation of matter." Protons and electrons, of which material atoms are compounded, may come together in some way and disappear, being converted into high-frequency radiation. But, again, this is emitted into space, is absorbed by other material bodies, and so becomes converted into the low frequency of heat, which again becomes ever more uniformly distributed throughout interstellar space.

And so, considering the elements of the universal system of things as quanta of energy it appears that the distribution of these quanta, or elements, tends always to become more and more uniform in all regions of space. The probability that we shall find just as much energy in any one block of space as in any other block, taken at random, becomes ever greater. And, looked at in another way, cosmic evolution means that a particular order, or arrangement, that of the concentration of energy in particular minute parts of the cosmos (in the stars) tends to disappear during those physical changes which we see to proceed in the universe. Since all that we call " physical phenomena " are dependent on the existence of these concentrations of energy, or of an initial, particular order, or arrangement, the changes that proceed in the process of cosmic evolution tend toward the cessation of those changes themselves, that is, to an ultimate equilibrium.

89*a*. Planetary Evolution. A planet was originally a certain mass of hot vapour extruded by a star as the result of the near approach of another star : the mutual gravitation of the two bodies led to the extrusion of material by one or both of them. This hot material drew together, in spherical form, condensed to a liquid and then to a solid state, cooling all the while. Finally a solid, light, lithospheric envelope, or shell, condensed on a solid, heavy metallic kernel, or centrosphere. Later water condensed on the lithosphere, or earth-crust, as the hydrosphere, or ocean. Finally an atmosphere came to surround the lithosphere and hydrosphere. Such has been the course of evolution of the earth.

The inorganic earth-envelopes. We shall now consider the formation of lithosphere, hydrosphere and atmosphere in order to contrast the processes with those by which the *biosphere*, or earth-life, was formed : it will be seen that the contrast of two

tendencies is displayed here also. When the lithosphere (and hydrosphere and atmosphere) were formed certain physical changes in a system of parts, or elements (the vaporous constituents and their energies), occurred and the consequence of these was the appearance of the envelope (say lithosphere). Now we may divide up the whole earth-crust into blocks (of, say, 10,000 cubic miles of volume each), and it will be easy to show that each such block is, *on the earth-scale*, very similar, in chemical and physical nature, to any other block taken at random. That is to say, the probability of uniformity of aspect of the parts of the lithosphere is great *and tends always to increase.*

So also with the hydrosphere and atmosphere. Thus the tendencies of the changes in an initial physical-chemical system that have led to the appearance of the earth-envelopes are similar to those that apply to stellar evolution.

89*b*. CHEMICAL EVOLUTION. What has occurred in the formation of the earth-envelopes is essentially what occurs when chemical substances react with each other. When, for instance, coal burns carbon and hydrogen combine, or react, with oxygen and heat is evolved. It used to be said that carbon and oxygen, hydrogen and oxygen combined to form CO_2 and OH_2 because the carbon and hydrogen " had affinity " with oxygen. We say now that the condition for such combinations is that energy dissipates. When C and O_2 unite, the reactants, C and O_2, have initially more internal energy than the resultant, CO_2, and the balance of energy is represented by the heat given off during the combustion. Initially the energy may be regarded as concentrated in the C and O_2, but after the reaction it is emitted to the surroundings, when the distribution of the resultant (the gas, CO_2) and the energy (heat) has become more probable. That is, if we sample the region all round the place where the reaction has occurred it is much more probable that we shall find the elements of the system (C, O, and energy) than before the reaction.

The chemical constituents of a system thus evolve towards states in which the elements and the involved energies tend to more probable states of distribution. In the course of this evolution the elements gradually attain chemical equilibrium, when they cease to react.

Chemical atoms themselves evolve in that they disintegrate by radio-active transformations. This is notably the case with

uranium and radium atoms, but it may be regarded as going on, very much more slowly, in all kinds of atoms. In the course of these changes the bound energy of the atoms is liberated as high-frequency radiation, but this suffers dissipation by absorption into other substances and ultimately it transforms into the low-frequency radiation of heat and tends to become uniformly distributed throughout cosmic space.

And thus the materials and energies that constitute the stars, cooling and shrinking planets and chemical substances tend always from states in which these elements (the materials and energies) are concentrated, or are arranged in improbable configurations, towards states in which the concentrations are levelled out, or in which the elements become arranged in the most probable configurations. These tendencies of inorganic evolution are clearly illustrated, in a trivial way, of course, by the disappearance of the configuration of a Patience card-series, when shuffling is carried out.

An important result: *In all inorganic evolutionary processes the probability of the arrangements of the parts, or elements, of the system concerned increases. Now it can be shown that the entropy of the system must increase as the logarithm of the probability increases.*

90. *ON THE TENDENCY OF ORGANIC EVOLUTION*

First we shall consider the formation of the " biosphere," that is, the concentric layer of living organisms inhabiting the soil, ocean and fresh waters, and atmosphere (that is, the lithosphere, hydrosphere and atmosphere). As to the origin of living things on the earth we know nothing. It is simplest to assume that, just as the primary vapours of the planetary mass fell together, condensed and chemically transformed themselves into the lithosphere and hydrosphere, so other vaporous constituents fell together and reacted chemically with the materials of the other envelopes so as to form the biosphere—that is, the first living organisms capable of reproduction. The difficulties of such an assumption are overwhelming, but it has been customary to make it and for the moment we accept it. The earth, then, became populated with simple organisms of the same kind, at some period of about 1,500 to 1,000 millions of years ago. It is the simplest

and most reasonable assumption to make that all these primitive organisms were of the same kind and were distributed with the same degree of uniformity as the materials of the lithosphere.

Organic evolution proceeds and we know enough of its history to convince us that its tendency is for simple organisms to become more complex and for an initial phase of uniform distribution to become replaced by later phases in which the distribution became much less uniform. If we divide up the surface of the earth into regions and sample these at random we shall certainly find that it is very improbable that any two regions taken at random will contain the same kinds of organisms. Therefore a distribution of the elements of a system that was initially probable has become very improbable because of its evolution.

Next we may take a developmental process, say that of a plant seed. The organism, or seed, is at first simple in structure but, as its development proceeds, it becomes more complex. It is a very small body, say an acorn, but it becomes a great tree. The substances of this body (water, CO_2 and simple mineral salts) were originally chemical molecules that were simple in configuration and were widely diffused throughout the lithosphere, hydrosphere and atmosphere, but as the development proceeds they become more and more concentrated, in the body of the tree, as chemical molecules that are complex in configuration. The energy that became embodied, in the potential mode, in these complex molecules was initially widely diffused in space as solar radiation. Thus configurations and distributions that were probable ones have become much less probable in the course of organic development and growth.

These examples will show what is the tendency of all organic evolutionary processes—the analyses of other particular examples of such process lead to essentially the same result. There is always some aspect of an organic evolution which shows that *distributions and configurations of the organic system considered become less and less probable as the evolution continues. And with this decreasing probability the entropy of the system also decreases.*

The entropy may be regarded as a function that describes the interchanges of energy between the evolving system and all the other things in its environment. The entropy of the universe, *as a whole*, continually tends towards some future maximal value and this means that energy that is available for transformations

(or events, or physical changes) continually becomes unavailable for such happenings, or the universe, as a whole, runs down. These statements also apply to such limited parts of the universe as a star, a cooling planet, chemical substances that have potential energy and radio-active atoms. When we apply the entropy-concept to organic evolution we have also to consider the energy-exchanges between the system that evolves (say the acorn) and the environment. We find that although (in the long run) the conclusion of *universal* entropy-increase holds good there is, in the evolving organic system *a local entropy-decrease.* This means that in this local, living system energy that would otherwise have become unavailable retains a certain fraction of its availability.

It is plain, therefore, that with respect to the entropy-law the processes of inorganic and organic evolution exhibit contrasted, or opposite tendencies.

91. *ON THE MEANING OF THE TERM "EVOLUTION"*

We can best discuss what we mean by " evolution " by reference to processes of individual organic development—since an organic evolutionary process is simply a series of developments in a race of organisms. There is differentiation in this series such that the individual, developmental processes change and so a race " evolves."

The term evolution obviously implies a previous " involution." Something that was rolled-up, wrapped-up, " latent," etc., becomes unrolled, unwrapped, " patent," etc. This was the original conception and it was replaced by that of epigenesis, which meant that something new, as regards bodily structure, came into existence in the developmental process. As we have seen (in Chapter VI) the epigenetic conception became accepted during that period when materialistic-energetic views were generally extended to all organic processes and the result was the revived conception of preformation, as it was applied to developmental processes by Weismann and, later on, in its present form, by Morgan and his followers. What were " involved " in an individual development were the genes and these particles, or agencies, or quanta, became " deployed," interacted with each other and with the environment so as to display an individual

embryogeny, or ontogeny. The genes were regarded as material, or causal, particulate agencies in the organic, bodily component called the germ-plasm. But it may be that individual embryogenies do not repeat themselves exactly and so a race of organisms may undergo transformism. Something is supposed to be involved in the transformist process and this is the occurrence of a " mutation "—a new gene, or genes, come into existence. How ? It has been observed that when breeding organisms are exposed to the action of certain physical agencies the development of the ova generated by them may undergo change so that the race undergoes transformism and this kind of effect is interpreted as due to the origin of new genes. Somehow or other the environment " induces " change in the genes. It is, then, new genes that are involved in evolutionary processes.

91*a*. EMERGENT EVOLUTION. It is not compatible with the extension of material-energetic conceptions to all organic phenomena that change should just occur and without some material-energetic " cause." On the other hand, the amplification of the conception of evolution to include the origins, say, of mentality, the religious feeling and God is difficult if we are to trace such evolutionary changes to genes induced by the agencies of the environment. It has been said, then, that such products of evolution simply " emerge." As an example of emergence the formation of water from the gases oxygen and hydrogen is taken. The " reactants " are $O_2 + 2\ H_2$ and the resultants are $2\ H_2O$. But there is said to be something in the water that was not in the reacting gases : the " property " of liquidity is said to " emerge " from the reaction of the gases, $O_2 + 2\ H_2$. It is not difficult to see the confusion in this notion. We imagine a " Newtonian universe " of mass-points (atoms) moving in accordance with Newton's laws and attracting or repelling each other with forces that are functions of their distances apart. Each mass-point is given position and force-co-ordinates (6 in all) and we have the system, $O_2 + 2\ H_2$. If now there are changes in the co-ordinates we have the system $2\ H_2O$: the system $O_2 + 2\ H_2$ " appears " to us as a mixture of gases and that which we call $2\ H_2O$ " appears " to us as a liquid, but since we assume some satisfactory resolution of the " mind-body " problem in both phases we may let the " appearances " cancel out and simply say that the property, liquidity, *is* the change of co-ordinates in

the system. Again, we deduce from the gas-laws that the entropy of a system of molecules is a function of the thermodynamical probability ($S = f(w)$), and we deduce from such statements that entropy (S) is proportional to the logarithm of the probability. Clearly, however, there is nothing in the terms of the latter equation that was not in the terms of the former ones. What "emerges" during the investigation is a new relation between the terms *and that we have made.*

Plainly, then, emergence is only a confused notion with regard to evolution and it does not help us in understanding the problem.

91*b*. Evolution simply regarded as Change. We say that inorganic nature "passes" and becomes "made" (Chapter I). Nature passes from the state of a cosmos towards that of a chaos, when we regard it as "made," because the state of chaos has greater probability than that of cosmos. In the passage there is continual change with tendency. We feel impelled, by our scientific fashion of post-Newtonian times to envisage a something that changes so that any phase in the process is dependent on the preceding phase: in that way we are able best to describe the passage of nature. Still that which is inorganic nature is essentially change with tendency.

Organic nature also proceeds. We see it to do so in the observation of a long series of ontogenies. An animal reproduces and the ovum passes through a series of changes which culminate in the appearance of another animal which is recognizably of the same kind as its parent. This progeny reproduces again and the same process of development recurs and so on through, it may be, millions of ontogenies. If, in some terms of this series of life-histories the ontogeny changes, in the way that we call inheritable change, a new kind of animal originates and there is racial change, or evolution. We now apply the scientific method which originated with Galilean mechanics and we seek for antecedents of these changes. Current biological thought attributes development and racial evolution to parts of the materials and agencies in the ovum and it holds that these parts interact with each other and with the materials and energies of the environment so that the parts become assembled as the organism—obviously neglecting the necessity for some agency that assembles the parts. This agency cannot be thought about as other than *the organism that itself changes.*

But, both in inorganic and organic evolution *something is involved*—because the processes are different ones. That which is involved in the passage of inorganic nature is tendency to increasing randomness, or greater probability of state. That which is involved in organic evolution is what we can only call "anti-randomness," or tendency towards retention of the initial phase of particular cosmic arrangement. Organic evolution expresses this tendency towards something in nature that is improbable in occurrence, all inorganic evolution expressing the tendency toward arrangements of natural things that are indefinitely numerous and therefore highly probable.

91*c*. EVOLUTION AND "PROGRESS." It is not merely humanistic tendency in thought that impels us to regard the main lines of organic evolution as indicating "progress." We may think of all evolution as leading "up" towards man, even when we remember the episodial changes that have led to the extinctions and degenerations of many races of organisms. In the evolutionary career the striking thing is the ways in which races of organisms have, on the whole, tended towards ubiquitous distribution, toward complexity of functioning that, more and more, gives them dominance among other kinds of organisms and greater mastery over inorganic nature—that enables them to express more and more opposition to the tendency towards the dissipation of energy that is the characteristic feature of cosmic evolution. It is in this sense that we speak of organic process as a tendency towards progress.

92. *ON HYPOTHESES OF EVOLUTION*

In the chapters on heredity and transformism we have attempted descriptions of the organic evolutionary process as it is understood in current biological thought.

i. Lamarckian evolution. Organisms, *in themselves*, change their modes of activity in response to changes in the environment, or as they migrate into new environments, or as they endeavour all the more to master an approximately constant environment. Successful responses mean that organisms that make them live longer and reproduce more often. The responses are not impressions made by the environment on the organisms—they are in themselves organismal changes with tendency. If they are

inherited (which is denied by many investigators) there is organic evolution.

But obviously Lamarckian evolution means individual organismal change with tendency.

ii. Darwinian evolution. Organisms, in themselves, display randomly occurring changes and such randomness is inherent in the organismal make-up. If some of the random changes in activity are inherited by the progenies of the individuals in which they first occur there is evolution. This is because some of the random changes are " selected," which means that organisms and their progenies have changed so that they may become more ubiquitous in distribution, live longer and reproduce more often. Not all random and inheritable changes have such effects and therefore in Darwinian evolution there is individual organismal change with tendency.

iii. Evolution by special creation. This means, it would appear, that the novelties, or changes, in organic life-histories are to be regarded as " acts of God." But since the novelties appear to have occurred as sequences that have tendencies the creative acts cannot be regarded as arbitrary, or random ones. It has been said that organic evolution may be thought about as the working-out of a creative thought in the Divine mind. We do not know, of course, what we mean by God *in this connection* except as an agency that operates in nature and we can only regard the results of that agency as individual organismal change with tendency. On ultimate analysis (so far as we can proceed with it) it is therefore difficult to say in what essential respect the hypotheses of evolution that we have considered differ from each other.

Except in this way—and here we find two ways of thinking about our problem. Formal religions include the idea that the Divine agency may only be modified by supplication, or prayer : thus we contemplate the processes of evolution rather than attempt, by our own efforts, to modify them. On the other hand, science may be regarded not only as the search for truth, that is, the discovery of whatever there is in the external world (whether the discovery be useful or not), but also as the attempts by man to modify the course of events in the external world (whether, or not, such modifications are useful to us). Scientific men believe that they are (however slightly) influencing the evolutionary process by experimental interference and the idea that there is

such a process and that it may only be modified by prayer to a Divine agency may be repugnant to them—as scientific men, of course.

iv. A Résumé. We believe then :

(*a*) that there is some agency in the ovum, spermatozoon, spore, bud, or other undeveloped organism, that evolves in the course of the developmental process. This is the " organization " and we do not know what it is. In the course of the development the undifferentiated organism evolves so that, by interaction with the energies and materials of the environment, it assumes the functional-structural configuration that is described by the characters of a species. The organization we regard as an ensemble of potentialities and this ensemble is a different one in the ova, spermatozoa, spores, buds, etc., of every organic species.

(*b*) Changes may occur in the organization so that the potentialities change. Every such change is called a " mutation." We associate the potential change with the parts of the undeveloped organism called the " germ-plasm," " chromosomes," etc., but we do not know what, physically speaking, is the change. Having once changed the same change is " inherited," that is, it reappears in the next generation of ova, spermatozoa, etc. If the change tends towards longer life and greater power of reproduction " selection " is said to have occurred and evolution, in the Darwinian mode, takes place.

(*c*) The developed organism has still, to some extent, the potentialities of change and it may, as the expression of some " needs or desires," change its methods of behaviour and functioning, and also its structure. It is believed that such changes, acquired by the developed organism, may affect the potentialities of its ova, etc., so that the acquired change may become an inheritable one. If the change leads to longer life and greater power of reproduction selection is said to have occurred and there is evolution.

(*d*) These hypotheses of evolution are still largely logical ones and are the subjects of controversy.

We have now to discuss the evolutionary process as something that has actually occurred. The evidence that an evolutionary career has occurred is the existence of records of life, in the past, in the forms of fossils. We have, first, to interpret the natures

and occurrences of fossil records in the light of morphological results, believing that structural resemblances between different kinds of organisms are indicative of genetic affinities. Then we have to display the results of such investigations in the forms of the sequences of races of organisms that, we believe, inhabited the earth in the past.

II. ANIMAL AFFINITIES

Rational classifications are based on *structural* likenesses and unlikenesses and not on merely superficial appearances of similarity and dissimilarity in animals regarded as wholes.

Superficial characters. Superficial resemblances may be illustrated by (1) a porpoise and a large fish ; (2) a blindworm (*Anguis*) and a snake ; (3) the tails of a fish and a whale. Although a similarity exists between the members of each pair noted, these members belong to different classes of vertebrates. Superficial dissimilarities may be illustrated by the cases of a garden snail, a limpet and a whelk. These animals are very different in appearance and habit, yet they all belong to the class of molluscs —gasteropoda.

Trivial Characters. Mendelian races, local races, varieties of species, species and even genera are characterized, in the classifications by differences of structure that are said to be trivial. Such characters are colours and colour patterns ; shell markings and " ornamentation " ; arrangements of feathers, hairs, scales, spines, etc. ; numbers of repetitional parts such as the scales, or finrays in a fish, or the joints in the antennæ of a copepod ; relative sizes of bodily parts, etc. These are structural characters, but they may be of the same general nature in widely different classes of animals. Thus the teeth-patterns are important (though " trivial," in the special sense) characters whereby the mammals are classified into families, genera and species, but much the same patterns are also utilized in the classification of the marsupials. Relative sizes of bodily parts may be employed both in the separation of species of fish and nematode worms. Numbers of repetitional parts are used to make fish-species (scales and finrays) and also copepod-species (the antennal jointing) and so on.

Tectonic Characters. These express the fundamental bodily structure. Thus absence or presence of a notochord (inverte-

brates and vertebrates); respiration by means of lungs or gills (mammals, sauropsida, ichthyopsida); bivalved or spiral shells (lamellibranch and gasteropod molluscs) and so on. These tectonic characters are, as a rule, unique, the occurrence of each diagnosing some one category of animals. They are the manifestations of body-building. They are usually not apparent on mere inspection of the intact animal but must be discovered by dissection and by investigation of the developmental history.

93. *ON HOMOLOGIES*

Such structures as the notochord of an *Amphioxus* and that of a Hag-fish are said to be *homologous*. The swim-bladder of a fish and the lungs of a mammal; the endostyle of a Tunicate and the thyroid gland of a mammal; the flipper of a whale and the forelimb of a rabbit; the pineal gland in man and the median, undeveloped eye of a lizard—these are all pairs of homologous structures. The blastodermic vesicle, in the development of a mammal and the blastula of an amphioxus are homologous phases in embryogeny.

93*a*. The Criterion of Homology. Structures that have the same origins and initial modes of development are said to be homologous. In a general way an established homology suggests that the structures involved have a fundamental significance that is the same, but we can only give precision to this notion by making the above definition. We *stipulate*, then, that the criteria of the homology of two structures are their similarities of development.

93*b*. Tectonic Characters express Homologies. The characters that are used in the major classificatory systems are tectonic ones and involve homologies. Thus the notochord, an axial stiffening rod, is of great tectonic importance in the structure of the bodies of very many animals. Wherever we find this structure and are able to trace its development we find that this is always the same—the notochord originates in embryogeny as an invagination of endoderm. Therefore it is homologous in all chordate animals. On the other hand, the eyes of the mollusc, *Pecten*, and those of the vertebrates exhibit certain curious resemblances, but these organs develop in very different ways and so we say that they are not homologous structures.

Vertebrates and lamellibranch molluscs are therefore not closely related to each other in classifications, in spite of the resemblances of some eyes in the latter group to eyes in the former one.

94. *ON THE PRIMARY HOMOLOGIES*

i. All nucleated cells are homologous structures. We make this statement, although we cannot apply the criterion of homology to nucleated cells—the history of which is unknown. But most nucleated cells are very much alike, in that they divide (mitotically) in the same, very special way. They are capable, as single cells, in appropriate conditions, of independent existence and of reproduction by mitosis. (Tissue-cultures in artificial media demonstrate this in very many cases.)

ii. A blastula-phase occurs in the embryogenies of most multicellular animals and this phase is homologous wherever it occurs. In very many cases, drawn from very many different animal groups the blastula is typical in mode of origin and form. When it is not typical the deviations can be accounted for, say, by the influence of food-yolk in the segmentations, or by precocity of potencies in the blastomeres. It is evident that animal embryogenies are " constrained," by something in the physico-chemical conditions, to take a certain typical course—that resulting in the formation of the blastular form.

iii. All gastrula-embryos and phases in the development of multicellular animals are homologous. The essential features in the process of a gastrulation are these : (*a*) the surface is increased by the invagination ; (*b*) Cells with different potencies are segregated as endoderm and ectoderm *or* such segregation confers different potencies on the cells ; (*c*) an internal, digestive cavity is formed by the invagination of part of the blastular wall so as to form the archenteron.

In spite of deviations from type due to yolk in the ovum, or to segregation of potencies in the ovum before cleavage occurs, gastrulation is the same fundamental process in most animal embryogenies. Therefore we conclude that all gastrula-phases are homologous and that the primary embryogenic cell-layers, endoderm and ectoderm, are everywhere homologous.

iv. The three germ-layers are homologous in all embryogenies. There are different ways in which the mesoderm originates—it

may arise from cells budded off from the junction of endoderm and ectoderm, or it may arise as vesicles budded off from the endoderm. But a third formative layer, the mesoderm, arises from one or other of the two fundamental germ-layers. This third layer we regard as everywhere homologous in the multi-cellular animals other than the Porifera and Cœlenterates.

94*a*. The Primary Animal Classification. We may utilize the above homologies in order to make a general and primary classification, which is as follows :

					Primary Animal Groups.
THE ANIMAL KINGDOM	*Protozoa* (1)				Protozoa
	Metazoa	*Metazoa without tissues* (2)			Porifera
		Metazoa with tissues	*Diploblastica*		Cœlenterata
			Triploblastica (3)	*Acœlomata*	Platyhelminthes, etc.
				Cœlomata (4)	Worms
					Polyzoa, etc.
					Echinoderms
					Molluscs
					Arthropods
					Chordates.

Here we see :

(1) The primary subdivision of all animals into unicellular and multicellular forms : the separation we base on the embryological result that a unicellular organism—the ovum, becomes multicellular in the process of segmentation.

(2) The division of multicellular animals into those in which segmentation results in a multicellular body where there is no distinct differentiation of cells into tissues. For a time this is so in all animal embryogenies and in the cases of the Porifera (sponges) the fully developed organism consists essentially of cells (the " collar-cells ") which exercise all the ordinary animal functions and are all the same in structure. In the rest of the sponge body there are obscurely differentiated supporting structures but no true tissues. The phase of the blastula roughly corresponds with this animal division.

(3) Tissued animals are separated into those with two developed germ-layers, the endoderm and ectoderm (*Diploblastica*) and those

with three such layers, the endoderm, ectoderm and mesoderm (*Triploblastica*). In embryogeny we see the distinction: the gastrula is diploblastic, but upon the formation of the mesoderm it becomes triploblastic. In the fully developed animals the Cœlenterates represent the diploblastic phase and the other primary groups the triploblastic one.

(4) Triploblastic animals are divided into those in which there is a cœlom, or body cavity, in the mesoderm and those in which this cavity cannot be recognized. And the distinction can be observed in some embryogenies. For a time the mesoderm may be solid and then follows a phase in which it attains a cœlomic cavity.

We are now left with the primary groups of the animal kingdom —the *phyla*, or other categories. No investigations made so far enable us to relate together in any other way the cœlomate phyla —at least no attempts to do so have been generally accepted by zoologists.

94*b*. The Parallelism of Embryological Phases with Classificatory Groupings. Clearly the embryonic phases occur in the following order (as, for instance, in *Echinus* and *Amphioxus*).

Unicellular	*Multicellular* and *Diploblastic*	*Triploblastic*	*Cœlomate*
The unsegmented ovum	The gastrula	The gastrula with mesoderm	The mesoderm with a cavity
(1)	(2)	(3)	(4)

And the order is also that of the degrees of generality of structure (as numbered) in the classification. But this is inevitable, for we have based the classification on homologies that are founded on embryonic phases.

95. *ON GENERALIZED TECTONIC CHARACTERS*

All organisms whatever, are, at the beginning, *or* all through their life-histories, unicellular. All multicellular animals pass through a phase of development which is typically, or atypically, gastrular. All animals that are " higher " (or more elaborated, tectonically) than the cœlenterates pass through a further developmental phase in which a third germ-layer is added to the two

fundamental ones. Thus there are *degrees of generality of developmental phase.*

All chordate animals whatever have, in their early embryogeny, an axial, stiffening rod that arises as an endodermal invagination. In the cyclostomes this notochord remains throughout life as the functional skeleton. In the Fishes the notochord acquires annular, calcareous rings ; then it becomes replaced by bony segments, or vertebræ, and in the most specialized vertebrates the vertebræ become very complex.

All vertebrate animals have a propulsive circulatory apparatus which consists of 2 muscular dilatations of the main blood-vessel. In the Fishes the dilatations become the muscular heart consisting of auricle and ventricle. In the amphibia the originally single auricle becomes divided into right and left auricles and then, exceptionally in the Reptiles and universally in the Birds and Mammals, the ventricle also becomes divided. Therefore there is the series :

2-chambered heart	→	3-chambered heart	→	exceptionally 4-chambered heart	→	universally 4-chambered heart
(Fishes)		(Amphibia)		(Some Reptiles)		(Birds and Mammals)

The generalized tectonic features in these examples are the notochord and the doubly dilated, muscular, circulatory apparatus—successive modifications elaborate these structures. Thus there are *degrees of generality of structural, or tectonic characters.*

It is this conception of degrees of generality of character that receives expression in rational classifications.

95*a*. THE CLASSIFICATION OF THE CHORDATA. The main divisions are so constituted :

Chordata	*Acrania* . .	Notochord present	N
		Nutritive organ, the endostyle present	E
	Craniata . .	as above	N(E)
		also a cranium present	C
		and a dorsal nervous system . . .	Dn
Craniata	*Cyclostomata* . .	Craniata as above . .	N(E)C Dn
		Mouth is suctorial	
		Branchiæ (gills) are present . .	Br
	Gnathostomata .	Craniata as above . .	N(E)C Dn
		Branchiæ present	Br
		Jaws in the mouth	J

Gnathostomata	*Ichthyopsida*	Gnathostomata as above	N(E)C Dn Br J
		an air bladder present . .	A or (A)
		Branchiæ may change .	Br or (Br)
	Sauropsida	Gnathostomata as above	N(E)C Dn (Br)J(A)
		The air bladder is a lung . .	(A)
	Mammalia .	Gnathostomata as above	N(E)C Dn (Br)J(A)
		Mammæ present	M

Symbols (on the right) denote the characters. When a symbol is enclosed in brackets, this means that the structure and functioning of the structure has changed—thus :

E = Endostyle ; (E) means endostyle that has become thyroid gland.

Br = Branchiæ ; (Br) = branchial arches that become parts of the hyoid or jaw skeletons, etc.

But, being the same in development E and (E) ; Br and (Br), etc., are pairs of homologous structures.

We can now make the formal classification according to the degrees of generality of tectonic structures.

Chordata	*Acrania*			Tunicates, Amphioxus, etc.	N E
	Craniata	*Cyclostomata* . . .		Lampreys, Hagfishes .	N(E)C Dn Br
		Gnathostomata	*Ichthyopsida*	Fishes .	(N)(E)C Dn Br A
				Amphibia	(Br) J(A)
			Sauropsida	Reptiles . Birds .	(N) (E)C Dn (Br)J(A)
			Mammals	Mammals	(N)(E)C Dn (Br)J(A)M

In such a classification we have a root and its divergences. The root is represented by the most generalized of all the characters that are considered—the notochord and the pharyngeal organ, the endostyle. As such these organs characterize the lowest chordates—the Acrania. The addition of a cranial skeleton gives the Cyclostomata, where the notochord is still present in the adult condition but where the endostyle begins to undergo change. Then a jaw-skeleton becomes added to the cranial one, which was all the head skeleton in the Cyclostomes, and so we get the Gnathostomata. Thus the jaw-skeleton is less generalized than the cranium which again is less generalized than the notochordal apparatus—and so on—the same method is applied in all the details of classification of the terminal groups of the scheme of p. 285, that is the Tunicates, Amphioxus, the Cyclostomes, etc.

96. *ON HOMOLOGIES AS INDICATIVE OF AFFINITIES*

Such a series of descents as is represented in the following scheme may easily be observed :

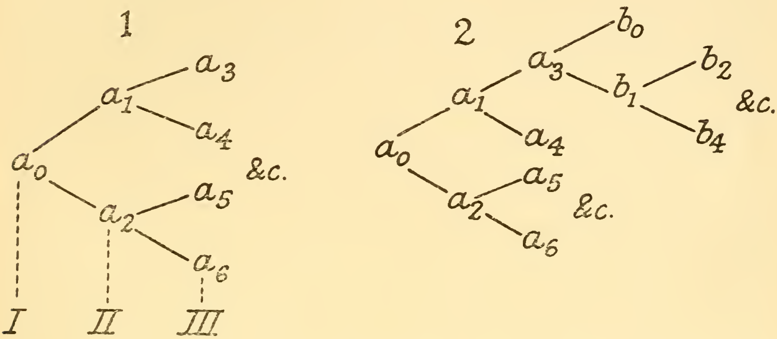


FIG. 36.

Here (case 1) is an " ancestor," a_0, which gives origin to the ova that become the progeny a, and a_2 ; a_1 similarly gives origin by reproduction to a_3 and a_4 and so on. All the organisms a_0, a_1, a_2, etc., are adults and present the same assemblage of characters, and these adult individuals are related together by the various ontogenies, or individual developments, represented by the oblique lines.

Now these ontogenies are *highly conservative processes* : thus a series such as the above one may extend to hundreds of millions of terms. This is actually the case with the Brachiopods, *Lingula*, which have existed without appreciable change since Cambrian times. Transformism, however, must usually occur long before a series extends so far and we may indicate such a change by the diagram, 2 of Fig. 36. This means that at the stage represented by a_3 transformism occurs and the individual, or individuals a_3 have produced ova that develop into individuals having characters represented by b_0 and b_1. That is, *the developmental organization has changed* (whether by " mutation," or " direct " or " somatic " induction does not matter). Thus the series of developmental phases, or the ontogeny $a - a_3$, is not the same as the new ontogeny $a_3 - b_0$ which results from the change of developmental organization.

Consider how this developmental change is manifested: when transformism occurs the tectonics of the development undergoes change—*but this change is not a radical one.* Thus the axial skeleton of the cyclostomes is a notochord, or undivided skeletal rod with a continuous sheath, but the axial skeleton of a Teleost fish is a backbone consisting of articulating segments, or vertebræ. In the development of the vertebral column of a Teleostean fish the notochord is not, however, absent: it develops as if the definitive axial skeleton were going to be notochordal and then the cells of the mesoblastic somites proceed to form the vertebral rings. By and by the notochord becomes a mere vestige. So also the water-breathing animal acquires gills or branchiæ: these develop as pharyngeal clefts that become provided with a series of bony arches and gill-filaments. Now when the ovum that is going to become an air-breathing animal develops and becomes provided with lungs this branchial apparatus is still there although it never becomes functional. Nor do the lungs arise developmentally *de novo*: they are developed from the swim-bladder, which never becomes functional in an air-breathing animal. And the larval anlagen of the branchiæ become developed into the skeleton of the tongue, the Eustachian tube, some of the bones of the middle ear, etc.

Thus when transformism occurs the developmental tectonics become changed. New functions are performed by organs that develop from the anlagen of organs that are being superseded—in the functional sense.

And so ontogenies may be expected to record transformist events—to some extent, at least, and, therefore, homologies—which are based on developmental events (or ontogenies) must record (it may be imperfectly) these transformist events, and consequently animal affinities.

96*a*. The Conception of Recapitulation. This was that an individual development recapitulated, in abbreviated and distorted fashion, the evolution of the race to which the individual belonged: ontogeny was said to repeat phylogeny. A mammal, for instance, was regarded as exhibiting a piscine phase in its development—indicating that living and functional piscine animals were in its ancestry.

It is easy to demonstrate the crudity of the conception—when stated as above. There are embryonic structures in the mam-

malian embryo that cannot possibly have belonged to animals in the mammalian ancestry—the amnion, for instance, which is a membrane completely enclosing the embryo. So also the salmon larva has a large yolk sac attached to its abdomen and we cannot easily imagine an adult fish that had such a structure. The fœtal chick has a special structure on its beak which is adapted to break open the egg-shell when the chick comes to hatch. No bird that lived in the past could have had such a structure in its adult state. And so on.

Further, eggs, embryos and larvæ of all animals, at all stages are specifically characterized. A plaice egg, embryo and larvæ, are all recognizably plaice and cannot be confused with the egg, embryo or larva of any other fish. A rabbit does not pass through a piscine stage—at every stage of development it is demonstrably a rabbit—and no other animal species.

Nevertheless, the tectonics of a development is a very conservative process. In the course of animal evolution this tectonic process changed so that its result was some new animal form—as we have seen above—and the changes occurred in such ways that records have been preserved. Although lungs, and the bones of the middle ear, and cerebral hemispheres are present in a rabbit and not in the lower fishes yet we see, from the rabbit ontogeny, that the anlagen of the lungs are the same structures that are the anlagen of the swim-bladder in the fish ; the anlagen of some of the auditory ossicles of the rabbit are the same things as the anlagen of some parts of the fish branchial skeleton and the anlagen of the rabbit cerebral hemispheres are the same things as the anlagen of the piscine pallium. By " the same things " is meant, of course, that the pairs of anlagen develop in the same ways from the pre-existing embryonic parts—that is, they are homologous structures. This means that there are resemblances in the ontogenies of animals : the developments of different mammals—say a whale and a rabbit—are more similar than are the developments of a mammal and a fish and thus whale and rabbit exhibit closer affinities than whale and fish. And the developments of a mammal and a fish are far more similar than are the developments of a fish and a crustacean. Up to some phase, the developmental tectonics of many animals may be very similar and this is indicative of their affinities. The fact that we can discern piscine, developmental tectonics in the embryo of a mammal, but

no trace of crustacean or echinoderm tectonics (beyond, of course, the phase of the establishment of the three germ-layers) justifies us in deducing an ancestry for the mammals that included some animal living in water and breathing by means of branchiæ.

The fact that many embryonic phases are strictly individualized means that trivial characters are superposed upon structural ones. (It is highly probable that this individualization in ontogeny is universal and may be recognized given sufficient investigation.) Thus birds' eggs are obviously strictly individualized by the patterns and colours of the markings, nevertheless these markings are trivial characters.

97. *ON THE MORPHOLOGICAL METHOD*

This has been indicated above: it depends on comparative-structural investigations which must be controlled by physiological studies.

Thus the tendency in ontogenetic processes is to accelerate embryogeny. The conservatism of developmental processes is very great, nevertheless it is minimized. Gill (or branchial) clefts —actual perforations of the pharyngeal wall—occur, of course, in the ontogeny of fishes and amphibia and are accompanied by the formation of vascular gill-organs. In the Reptiles and Birds the clefts still appear in the development, but—since air-breathing by the lungs comes about—the actual, vascularized gills do not develop. In the higher mammals, however, the pharyngeal wall is never really perforated and only branchial cul-de-sacs develop and these only in so far as they are of tectonic significance in the development of, say, the Eustachian tubes, the thymus gland, and other organs. The development of the lungs is accelerated and the modifications of the typical piscine, branchial anlagen are directed more and more to those new organs that the ontogeny, so to speak, anticipates.

Recent research also indicates the influence of specific growth-stimulating agencies (hormones) on the rate of development. Further, this influence may be differential, possibly retarding some, and accelerating other embryonic tectonic processes. Such accelerating and retarding agencies may possibly be introduced into the ovum, *via* the spermatozoon, by selective matings. And

obviously the direct action of the environment is to be reckoned upon in ontogenies—and environmental changes consequent on adaptive behaviour, migrations, etc. Plainly the establishment of homologies from comparative-embryological studies may be fallacious unless it is accompanied by experimental-embryological investigations.

97*a*. PHYLOGENIES. Rational classifications thus *suggest* phylogenies. A phylogeny is a formal statement that indicates what have been the lineages, or descents, or blood-relationships of large groups of organisms. Thus the classification of the vertebrates given above may thus be restated.

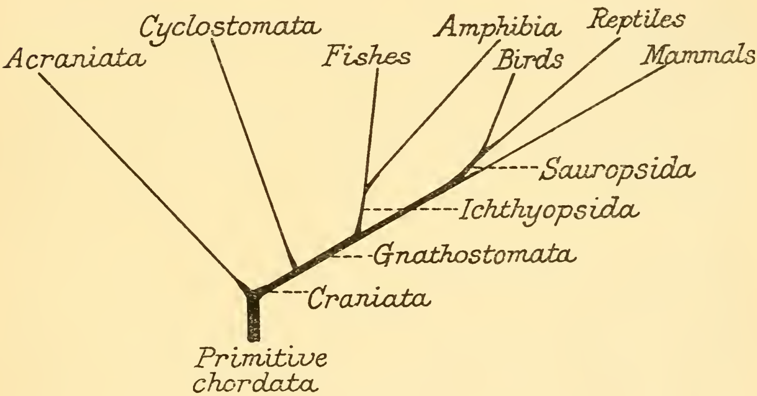


FIG. 37.

Here the root, and the divergences of the vertebrate stock, and the facts on which these are deduced are just the same as in the tabular classification, but the graphic way of presenting the facts suggests descent.

The statement, nevertheless, is not to be regarded as a phylogeny, or " genealogical tree." Presently we shall see that there " ought to be " an actual historical record of such a phylogeny in the data of paleontology. That record, however, is exceedingly imperfect in so far as it ought to present a general vertebrate phylogeny and the data of morphology are absolutely essential in constructing it. But imperfect as it is the paleontological record enables us to write the above phylogeny in a very

different way inasmuch as it gives a scale of the actual importance of the various divergences. To this matter we return.

And it will be seen that paleontology, being an imperfect historical record, and incapable of being reconstructed where the data have been destroyed, cannot of itself give us complete phylogenies. But this may not be so with the data of morphology —which may be sought in the intensive study of ontogenies and anatomical comparisons.

III. THE PALEONTOLOGICAL RECORDS

The remains of animals and plants are found in the sedimentary rocks and these remains are very often so perfectly preserved that much of the coarse and fine anatomy, and even of the embryological phases of extinct organisms, can be elucidated. Paleontological records, when considered along with the morphology of living organisms, may greatly extend the scopes of classifications; thus some fossil animal may exhibit the anatomical characters *a b c d e* (where the characters *b c d e* are those considered in the last sections. Obviously *a* may be a more generalized character than *b c* for this reason—there are other animals which exhibit the characters $\alpha\beta\gamma\delta$; therefore the character *a* is common to the two categories *a b c d* and $\alpha\beta\gamma\delta$. The fossil animal that exhibited *a* in addition to *b c d* therefore extends the phylogeny of the category *a b c d* in that it links this up with the category $\alpha\beta\gamma\delta$: it is therefore said to be an *annectant form.* Thus the fossil bird *Archeopteryx* had teeth—and no living birds have teeth. Reptiles have teeth and there are other anatomical characters in respect of which Birds are akin to Reptiles. *Archeopteryx* is therefore an " annectant form," linking together Birds and Reptiles.

Also it is usually the case that the more generalized character is also the more ancient one. Thus all living fishes have a notochord—either in the adult, or in the embryonic phases, and only some (though by far most) of living fishes have distinct, segmental vertebræ: therefore the notochordal, axial skeleton is a more generalized character than the vertebral axial skeleton. Now the axial skeleton of the most ancient (Silurian) fishes was a notochordal one.

And so the rational classification, based on a logical arrangement

of more and less generalized anatomical characters, has the same order as the time arrangement of embryonic phases, where the early stages are more generalized than the later ones. Fossil remains can also be arranged in a time-order and the earlier records present more generalized characters than do the later ones. We find, then, that the classificatory, ontogenetic and paleontological series display similar tendencies. These series are as they would be if they were the records of an evolutionary process.

98. *ON THE STRATIGRAPHICAL SERIES OF ROCKS*

The greater part of the body of the earth—up to a depth of two or three hundreds of miles from the surface—consists largely of metallic substances (iron, nickel, etc.). Superficial to this kernel is a layer of heavy basaltic rock and it is believed that this basaltic substratum comes to the surface, over the deep ocean bottoms. Embedded in the substratum are the continental earth-blocks. These consist mainly of relatively light igneous rocks. Covering them in many parts are large areas of sedimentary rocks.

The latter are conglomerates, breccias, sandstones, mudstones, limestones, etc. The latter consist typically of the skeletons of Molluscs, Echinoderms, Corals, Calcareous Algæ, etc., or they may be chemical precipitates. There are also carbonaceous strata (coals, lignites, etc.) and there may be porous sandstones containing petroleum. Such are the main categories of sedimentary rocks.

Generally they have been deposited, as particles of various sizes, at the bottoms of lakes or shallow seas. The particles have, typically, been carried in suspension in river water or in lakes, or in the sea, and then deposited. But the materials of sedimentary rocks may also be air-borne (as in blown sand). No sedimentary rock is known that has been deposited at the bottom of a deep ocean.

They are arranged as strata, originally laid down in nearly horizontal positions. Groups of strata make formations and groups of formations are systems. The sedimentary rocks can be arranged in a time-series and this is summarized in the following diagram.

Era.	Period or System.	Age in Millions of Years.[1]	Revolutions.	Life.
Cainozoic.	Recent			
	Pliocene	(37)		
	Miocene		Alpine	Mammalia; Angiosperms
	Eocene	60		
Mesozoic	Cretaceous	(59) 120	Laramide	
	Jurassic	150		all invertebrate phyla; vertebrata; Land plants
	Triassic	210		
Paleozoic .	Permian	240	Appalachian	
	Carboniferous	(204) 330		
	Devonian	420		Thallophytes; The fossiliferous period
	Silurian	450	Caledonian	
	Ordovician	540		
	Cambrian	600		
Proterozoic		(587)	Killarnean	some invertebrate fossils
			Algoman	Evidences of life but no fossils.
Archeozoic			Laurentian	
		(1257) 1200		

[1] Different methods give rather different results. Still the general similarity of order of magnitude is encouraging.

The table represents the durations of time occupied by the deposition of the various systems of stratified rocks, Recent, Pliocene, Miocene, etc., or included in each era—Cainozoic, Mesozoic, Paleozoic, etc. The whole period of sedimentation is the same as that throughout which there has been water on

the surface of the earth. The latter was, at a remote time from now, a mass of molten-gaseous material which broke away from the parent sun—that was probably between one and two thousands of millions of years ago. When this gaseous-molten mass solidified and became cool water from the primitive gaseous envelope condensed upon it and formed the first seas—that we take to be about 1,200, *or more*, millions of years ago. As soon as the first stable, solid crust and seas appeared there must have been erosion of land and consequent sedimentation.

The approximate ages of the various systems are given in millions of years. These results depend mainly on investigation of the rate of radio-active change which is imperfectly recorded in the compositions, and appearances presented by certain minerals. It is probable that the ages of the systems cannot be less than those given.

The process of sedimentation has not been a continuous one. Between some of the systems—as, for example, between the Proterozoic and Paleozoic rocks, as we know them, there are " unconformities," that is, there were other sedimentary rocks there that have been eroded and destroyed. At irregular intervals there have been geological " revolutions " in the course of which the seas have " transgressed " on the land ; large parts of the latter have been eroded ; mountain ranges have been formed—and eroded. In general great earth-disturbances have occurred. At present we live in the period of earth-quiescence that has followed the last (Alpine) revolution.

Throughout the entire period represented in the table life has been possible—and has probably existed, first in the seas and then on the lands. The table presents a general summary of the occurrence of life, but this we shall consider presently.

98*a*. Fossilization. Fossils are artifacts that result from the preservation, with alteration, of the hard or soft parts of the bodies of plants and animals. As a rule, it is the hard parts such as the shells of molluscs, the hard parts of Echinoderms, the scales and endoskeletons of Fishes, etc., that become preserved as fossils. But even leaves and the soft tissues of animals may exceptionally become preserved. In the ordinary processes of fossilization the dead body of the organism becomes covered by fine mud, or silt, that retards decomposition and may not crush the body. The shell, skeleton, etc., then, usually become mineralized, that is,

the original substance becomes replaced by enduring lime, silica, etc. In this way the fine structure of the body, or bodily part, may be more or less exactly represented.

Fossils may be impressions, or casts. Thus the marks made by the feet of Reptiles, Amphibians, Mammals, etc., when walking on soft sands, or muds, may become filled up by silt before the marks became obliterated.

So far as observations of the conditions of the present time show, the process of fossilization, so that definite artifacts may be formed, is exceptional. Putrefaction, crushing, etc., must, in the great majority of cases, lead to the destruction of animal and plant remains before the processes of replacement and mineralization have gone far enough to lead to preservation of the form of the body, or part. As a rule, the materials of organisms are almost completely dispersed after death. Proteins, fats and carbohydrates are, in time, resolved into CO_2, OH_2 and traces of mineral salts. Even the relatively resistant substances of teeth and hard bone become decomposed : so these substances—though they do occur are rare in the deep-sea clays, which are residues incapable of further change.

But sediments may contain organic remains, or may be such as they are because of organic activity, even although no definitely formed fossils can be recognized. Carbonaceous materials in rocks are held to be the evidences of life contemporaneous with the deposition of those rocks inasmuch as we do not know how otherwise these materials could be formed. Limestones that have no fossils may have been formed by precipitation of $CaCO_3$ from solution in sea-water and this precipitation has been the result of a change in hydrogen-ion-concentration brought about by the photosynthetic processes of planktonic plants. Flints and cherts appear to be formed by deposition of silica after some organic processes. Petroleum may be the result of decomposition, in special circumstances, of organic materials.

99. *ON THE NATURE AND LIMITATIONS OF PALEONTOLOGICAL RECORDS OF PAST FORMS OF LIFE*

Stratigraphical information enables us to reconstruct the past so that we can infer these things :

Past geographical conditions ; heights of the land, depths of the seas ; relative extents of land and water, etc.

Climates ; glaciations ; ice caps ; swamp, lacustrine and desert conditions, etc. ;

Earth-crustal disturbances ; mountain building ; vulcanism, etc., and thus the setting up, or the removal of barriers to the migrations and disseminations of organisms ;

Past faunas and floras ; the distributions and densities of organic populations ;

Kinds of organisms and their relative dominances ;

Habits of animals that lived in the past ; their anatomy (which can be inferred, by analogy, even if only some of the hard parts are preserved in the fossil form) ;

Phylogenies, or formal schemes of evolution ; and so on.

The limitations of paleontological evidence of evolution. But it is obvious that the evidence is, and must always be, very defective. Great numbers of animals and plants must die and leave no permanent records for every one that is fossilized. Vast masses of sedimentary rocks have been eroded away and redeposited as new sediments : in such cases the included fossils are destroyed. Stratified rocks have been metamorphosed by heat, pressure, etc., and their included fossils have become changed so that they cannot be recognized. The paleontological record is therefore defective and must remain so in spite of all investigation.

99*a*. PALEONTOLOGICAL SEQUENCES. So far as it goes, paleontology presents us with sequences of occurrences of fossil remains which are as they would be if a process of evolution had occurred. Let *A* be some morphological types preserved as fossils and let the accents of *A* denote progressive morphological changes : then we have examples of such series as the following one :

$$A — A' — A'' — A''' — A'''' — A''''' —\text{etc.}$$

Time—early——————→Late.

Thus the evolution of the horse is inferred from the series of fossils (the particular series is illustrative—there are several on the books) :

Phenacodus—a small ungulate	mammal	with	5 complete toes	A
Pachynolophus—	do.	do.	4 toes . . .	A′
Anchitherium—	do.	do.	3 toes and the vestige of a fourth one .	A″
Anchitherium—	do.	do.	only 3 toes . .	A‴
Hipparion—a donkey-sized		do.	1 large toe and 2 small ones .	A⁗

Equus—the modern horse with	1 large toe and vestiges of two others . . .	A′′′′′

and the time order is as follows :

A	——→A′	——→A″	——→A‴	——→A′′′′	——→A′′′′′
Lower Eocene	Eocene	Early Miocene	Late Miocene	Pliocene	Pleistocene

——→Time about 60 millions of years——→

This is a *major paleontological sequence* : the changes in morphology between stage A′′′′ and stage A′′′′′, for instance, are generic ones, corresponding roughly to the difference between a dog and a wolf.

Minor paleontological sequences occur and the magnitudes of the changes between stage and stage in them are of about the same value as those small changes called Mendelian ones. Examples are the changes in form of the septa in the Mesozoic Ammonites, or in the pores in the tests of sea-urchins of the same systems. In these latter sequences we probably see the actual steps of the evolutionary process—the elements of transformism themselves in permanent record. In the major sequence illustrated above we see, between stages A′′′′ and A′′′′′, that is, between *Hipparion* and *Equus* a morphological change in which the 2nd and 4th toes became reduced to the vestigial bones that we find in the present-day horse. We do not suppose that this change occurred all at once, that is, that a three-toed horse had offspring showing only one functional toe. Either on the hypotheses of Lamarckism, or on those of natural selection of small inheritable variations there must have been a long series of generations between *Hipparion* and *Equus* and in these generations the anatomy of the feet varied by very small steps—just such small steps as are seen in the series of Ammonities, or of sea-urchins mentioned above. In the course of this minor sequence the 2nd and 4th toes gradually diminished in size until they became small vestigial bones and at the same time the 3rd toe became gradually bigger until it became the functional walking one.

99*b*. Phylogenetic Histories. Such a series of forms, beginning with the Eocene *Phenacodus* and ending with the existing *Equus*, represents the phylogeny of the Horse, an Ungulate mammal which has specialized in a certain way (increasing size, tending to run speedily on great, grassy plains, exchanging

succulent marshy vegetable food for dry grassy materials, etc.). The full phylogeny would express all the other anatomical characters involved in the processes of transformism, but we only know the skeletal ones (including the teeth) from direct evidence.

As another example we may take the phylogeny of the modern, dominant Teleostean fishes.

Primitive Silurian Fishes
- Chondrichthyes—
  - Elasmobranchii
  - Holocephali
- Osteichthyes—
  - Teleostomi—
    - Modern Teleostei
    - Modern "Ganoids"
  - Dipnoi

and so on.

And reference to the records of paleontology will give series of major sequences that fit into this scheme.

Phylogenies, then, we assume to show the evolutionary histories of races of organisms—the directions and results of processes of transformism.

Paleontological records are used in two ways: (1) A fossil is the material from which we deduce the types of structure of an extinct animal so that we can include the latter in our classifications. A rational classification thus includes past, as well as present life. (The above classification of Fishes, if written out in full, would contain many groups that are now extinct.) In such a scheme the extinct forms fill up obvious gaps in the classification of living ones.

The paleontological records, besides filling up these gaps, *date* classifications: thus *morphology* leads us to infer that Birds and Reptiles are more closely allied than Birds and Mammals or Reptiles and Mammals. And the fossil Bird, *Archeopteryx*, shows Reptilian characters more prominently than any other living or fossil Bird. And *Archeopteryx* is the oldest known fossil Bird.

In the main phylogenies are based on the comparisons of structure in living races of organisms. Because of the exceptional and accidental nature of the process of fossilization it is the case that paleontological sequences, such as are mentioned above, are rather rare. Undoubtedly there are deficiencies in the record due to actual destructions of stratified rocks with their included fossils. But so far as they go, the fossil records enable us to infer that the logical order exhibited by phylogenies founded on structures of living races of organisms is also a time-order.

IV. THE EVOLUTIONARY CAREER

100. ON THE ORIGIN OF LIFE

It was a consequence of the materialistic philosophy of the last century that the "origin of life" was regarded as a problem to be solved by science. It was generally held that when the materials of the earth's crust had solidified and cooled so far as to allow of the condensation of the water of the atmosphere living things came into existence. It was thought that some of the materials of the lithosphere, hydrosphere and atmosphere became energized by solar radiation and then reacted with each other so that very simple organisms came into existence. It is, of course, certain that there was a phase of earth-history when living, protoplasmic things could not exist. But there is no plausible hypothesis as to the ways in which water, CO_2, inorganic nitrogenous and other mineral substances reacted on each other, *and of themselves*, so as to "synthesize living matter" and the arguments of Section I of this chapter will show how very unlikely, or improbable, it was that such syntheses did actually occur. At all events, no results of modern physiology have even tended to throw light on the problem.

And, of course, it may be the case that the problem is only a pseudo-one and that it is just as foolish to inquire into the origin of life as it would be to ask what was the origin of the universal tendency to entropy-increase. We have no doubt that the distinction, or degree of difference, between living and lifeless things is a problem for physics. And we have no confidence that the basal conceptions of physics have been established. That being so, it is futile further to continue this discussion. From the point of view of mathematical physics all that we can say about the origin of a living organism is that it must have been *an enormously improbable occurrence*.

101. ON THE EARLIEST FORMS OF LIVING THINGS

It is certain that conditions favourable for living things, as we know them, were present on the earth at least 1,000 millions of years ago. It is also certain that the oldest fossil remains are found in rocks that are little over 500 millions of years in age. Doubtless there were living things on the earth throughout all

the period when sedimentary rocks were being formed, but these earliest rocks have been so greatly metamorphosed that the fossils that they may have contained are no longer recognizable. Graphitic materials and calcium carbonate in certain forms occur in Proterozoic and Archeozoic rocks and there does not appear to be any other mode of origin of these materials except by organic processes. Again the very early forms of organisms were doubtless such that they were not easily preserved in fossil form. Therefore there are indications that living things existed in Proterozoic and Archeozoic times, but there is no evidence that enables us to ascertain what were their forms.

101*a*. THE ORIGINAL TERRESTRIAL PHYSICAL CONDITIONS. That being so, we can only speculate as to what the first organisms were in function and structure and even this speculation is strictly limited by lack of knowledge of the original terrestrial conditions. When the vaporous materials of which our planet was formed condensed a heavy metallic kernel, or centrosphere, first liquefied and over this was laid down the stony lithosphere, or earth-crust. As we know it now, this lithoscope is a complex mixture of silicates of aluminium, potassium, sodium, magnesium, with other metals in the forms of oxides, etc. Everywhere the uppermost layer of the earth's crust consists mainly of a "magma," heavy and basic in the lower levels and light and acidic near the surface. This magma we may regard as the original earth-rind. It is differentiated locally and it is overlaid locally by sedimentary rocks derived from its own disintegration and weathering.

The original sea. It has generally been held that the water vapour of the original earth-material condensed to form the ocean, which had then much of its present mass. But it is now known that molten magma at a high temperature can combine with water in a high proportion of the latter. Therefore it is probable that the original ocean was very small in mass and that the original dry land consisted of bare rock of the granitic type. Throughout geological time there have been earth-crust disturbances in the course of which molten magma came to the surface as larva outflows and in volcanic eruptions. When this happened the water that had been in combination with the magma became liberated, as steam, into the atmosphere, as the magma cooled. Therefore the volume of the oceans has gradually increased throughout geological time. It is also probable that the original

ocean was very saline, for sodium chloride and some other halides are volatile in steam at a high temperature. As the volume of the ocean increased it must, then, have become less saline.

The original atmosphere. We have some knowledge of the composition of the gases liberated when molten magma solidifies. We find, in the following order of abundance :

$$CO_2,\ CO,\ S,\ SO_2,\ Cl,\ HCl,\ N_2,\ H_2\ ;$$

and such may have been the composition of the original atmosphere. The sulphur would condense as solid ; the SO_2, Cl and HCl would combine with the solid materials of the earth-crust and there would remain CO_2, CO, N_2 and H_2. There would be no oxygen at first since all of it would have been used in oxidative processes. The first atmosphere that endured would therefore contain CO_2, CO, N_2 and H_2.

Thus the earliest protoplasmic organisms probably evolved in small, shallow, highly saline seas and not on the surface of dry land since that had still to undergo erosion and mature weathering. The gases in the atmosphere and in solution in sea-water were as above stated.

101*b*. The Original Modes of Metabolism. Such physical conditions present no difficulties for living things. Even at present we know organisms (Algæ, Fungi, Bacteria, etc.) that can (1) utilize CO_2 in the absence of chlorophyll, (2) can assimilate, or utilize, N_2 and also inorganic N-compounds, (3) can utilize, or assimilate S-compounds, probably carbon-compounds, such as coal, and also Fe-compounds, and (4) are anærobic, that is can live and function in the absence of free oxygen. These earliest organisms were probably unicellular ones, or they may have been plasmodic, that is, masses of protoplasmic material containing nuclei but undifferentiated into cells. In structure they were probably similar to the organisms we know, for there are no apparent cytoplasmic or nuclear differences between say, iron, sulphur or CO_2 assimilating bacteria : the original " life-substance " was capable of all these modes of metabolism. We do not know when chlorophyllian organisms first evolved and this was probably very early in earth-history. When they did evolve, the atmosphere would come to contain O_2 and this would oxidize the H_2 to water and the CO to CO_2. The water would condense into the ocean and the CO_2 would tend to decrease in amount as

the carbon assimilation habit became prevalent. Thus the atmosphere would tend to its present composition.

And as the volume of the ocean increased the processes of precipitation of water and snow would also increase. The bare surface of igneous rock would become eroded and weathered and true soils would appear. Then land faunas and floras would appear.

All this preliminary, but most significant, evolutionary process must have gone on during Archeozoic and Proterozoic times. Apart from those of Algæ and Sponges there would be no organic skeletons of mineral composition and therefore susceptible of fossilization. In all this vast period of time (nearly half of the whole life-period) hardly any permanent remains of animals and plants were formed and such as may have been fossilized are now irremediably destroyed by the extensive alterations of the Pre-Cambrian sediments. We have therefore no records that indicate what were the structures of the earliest living things and we can only doubtfully infer what may have been their modes of metabolism. It is certain that, at the beginnings of the Paleozoic period all the great types of animal and plant organisms (except the land plants) had been evolved. It is probable that these great types did not evolve from a single organic stock but from several such stocks, as is indicated by the various modes of metabolism that were possible ones.

We can therefore only attempt to describe the evolutionary career as it is laid open to us in the fossil remains that are disclosed in the Paleozoic and upper sedimentary rocks.

102. *ON "LINES OF DESCENT"*

We think of some natural region as being populated by animals of a particular kind, or species, all freely interbreeding and reproducing (as is generally the case, in the wild,) once a year. There are perhaps millions of individuals in the population and once a year a certain fraction of these reproduce so that there is a new " generation " of the species at about the same season in every year. On the average the population is constant so that as many individuals must die as are born during any specified period. Such a stock may continue to populate the region, remain constant in numbers and exhibit no change in characters,

or behaviour, for very long periods of time. As a rule, the same natural region will be populated by many kinds of animals and plants, but this does not matter in the present exposition. We may represent the succession of generations of the stock, year after year, by an unbroken straight line, or band (1, Fig. 38); the thickness of the band indicating the density of the population; its length indicating the period of time during which the population has existed and the continuity of the line, or band, suggesting that there has been no change in the characters of the individual organisms forming the species:

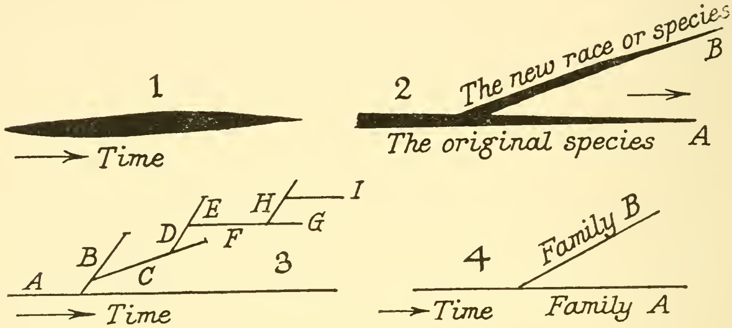


FIG. 38.

Now let a number of mutations occur so that, in a certain fraction of the population, the characters of the species change, a new sub-species, or variety, or race, coming into existence. We represent such a transformist process as in 2, Fig. 38. Next we may imagine that the transformist process continues, so that mutations appear among the individuals of the new race, and mutations among these latter kinds of individuals, and so on. We may represent such occurrences as in 3, Fig. 38, where A represents the original species, which continues to maintain itself unchanged. Just as the line B represents a new race originating in the first mutating individuals of A, so C represents another race originating in mutating individuals of B, and so on. The marking C, will indicate that the species, or race, C, dies out, or becomes extinct. Obviously at each branching the characters of the diverging species become more and more different from those of the original one, A. We may say that a group of species, G, H and I come into existence and these differ so much

in characters from A that we are justified in classifying them as a different family of organisms from that one to which A belonged. And so on with orders and classes. We may therefore simplify the last diagram as in 4, Fig. 38, and make the convention that a straight, unbroken line represents a family, or order, or class according to the minuteness of our classification.

If these methods were perfectly justified by the evidence (fossil records) that we have we might now construct *phylogenies*, or schemes of descent, showing the actual ways in which the various groups of animals have evolved from each other and from a common, original stock. Thus :

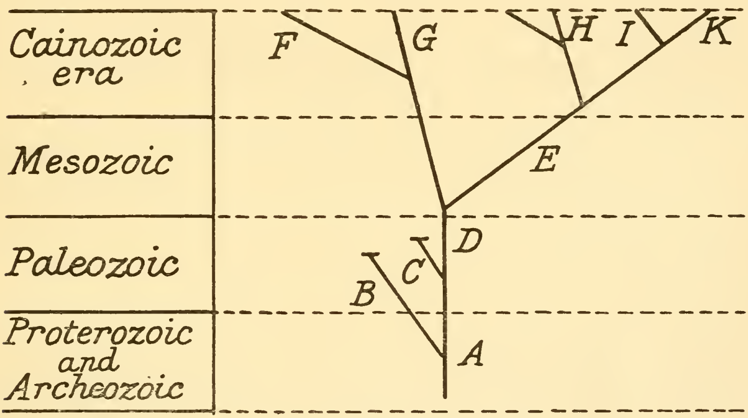


Fig. 39.—An Imaginary Phylogeny.

where the basal line A represents an original stock. From A a group of species, all resembling each other in certain common characters, has evolved : we call this group of species the class of animals B. This class consists of many species, each specific line really representing a great succession of generations of individuals. C is another such divergence from A. D and E represent two groups of species into which the common stock A has broken up and so on. The whole diagram might be said to be the representation of the phylogeny of the existing (in Cainozoic times) groups of animals F–K. It is, of course, a pure fiction and it may be said at once, that the records of paleontology do not enable us to construct such a scheme as applying to

the evolution of any groups of animals or plants: it only suggests the methods of representing in a diagram the successions, in time, of the kinds of animals found as fossils and their structural relations to each other.

What we are really justified in doing is to make such a diagrammatic representation of fossil records as that which follows:

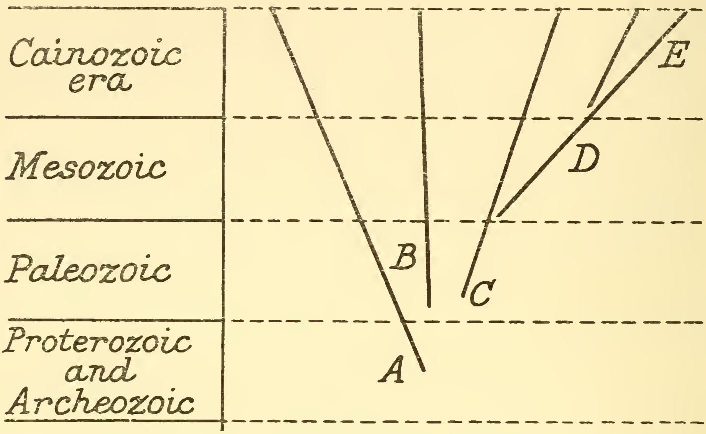


FIG. 40.—THE GRAPHICAL REPRESENTATION OF PALEONTOLOGICAL FACTS.

We find fossil remains of animals, A, that are all so structurally similar to each other as to justify us in including them all in the phylum, or groups of allied species, called A. These fossils are found in all the rocks of the stratigraphical series and we conclude that there has been an unbroken series of generations persistent since the upper Proterozoic times. Similarly with B and C. From the end of the Paleozoic periods we find fossils all of which so resemble each other that we group them together in the class D. But the structure of these animals D is rather like that of the phylum C: indeed we regard them as included in the diagnosis of C, but they are a special sub-group, or class, of C and so we make the line representing them converge towards C. So also with the line E, which represents a group of species, the structure of which is such that D includes it, but it is also such as to be regarded as a special sub-group, or order of D. So we make it converge towards D. These convergences are based on morphological similarities, as made out by study of fossil structure,

in the light of our knowledge of the structure of present-day animals, the hard skeletons, and perhaps other parts which can be compared with the fossil structures.

Such a representation of a phylogeny, based on the occurrences of fossil remains and of their structural similarities and differences, suggests the system of branchings of the twigs and main branches of a tree : the trunk of the latter representing some hypothetical common stock from which we infer that the various groups of organisms, represented by fossil remains, have diverged, or evolved. Actually, however, the picture that paleontology suggests is that of a system of divergent branches that do not actually meet in a trunk, but which converge to a trunk.

103. *ON THE MAIN FEATURES OF THE EVOLUTIONARY CAREER*

These are diagrammatically represented by figures which have been constructed on the principles indicated above. We see, then, that both in respect of animals and plants (Figs. 41–4) a number of main types of organisms appear to come into origin independent of each other at about the beginning of the Paleozoic periods (in the cases of the animals) and—with the exception of the Thallophytes—a little later in the cases of the plants. These main *types* of organisms, having once appeared, continue to maintain themselves up to the present times. In the history of each main type there have been " episodes " (Section 106) when " embroideries on the types " have appeared, have flourished and have become completely extinct, or have left only some unimportant modern representatives.

It would be wrong to suppose that the appearances of these main types were actually independent origins of living things, as the diagrams suggest. Such an interpretation is improbable in view of the great periods of time (Proterozoic and Archeozoic) which undoubtedly were such as to permit of life, but which are not represented by fossils capable of structural description. We must assume that there was a long pre-Cambrian period throughout which these main types of life were being evolved and when, it may have been, they did evolve from one original life stock. Still the possibility of the independent evolutions of various modes of metabolism must be borne in mind and, as structural characters are really made by these modes of functional

activity, we may plausibly infer that most of our main types have existed since the beginnings of life.

103*a*. THE MATERIALIZATION OF LIFE. In this Pre-Cambrian evolution life successfully manifested itself in the processes we have indicated: N_2-assimilation; the assimilation of N-compounds containing oxygen; CO_2-assimilation; S-assimilation; Fe-compounds-assimilation and probably in other metabolic modes. Thus life expressed itself in the chemical and physical changes that were carried on, with the aid of solar radiation, in compounds of carbon and nitrogen, and (to a less extent doubtless) in compounds of S and Fe. Very early in the history of the animate world life became an affair of the chemical activities of C and N because of what we may call the enormous versatility of these elements.

103*b*. STRUCTURAL MANIFESTATIONS OF LIFE. We have, of course, to consider the matter of the evolution of organic structure. To some extent structure is unessential: for instance, the simple unicellular organism such as an Amœba, a Diatom or a Peridinian, carries out all the functions of life displayed by the structurally complex metazoan or metaphytic organisms. Yet there has been an obvious evolution of structural forms and, in so far as this seems to be essential to evolutionary "progress," we must inquire as to what it means. Structural evolution, therefore, implies in the main the development of greater and greater size, on the one hand, and greater and greater mobility, on the other. Size is well illustrated by the difference between a pelagic, minute, unicellular alga and a rooted *Laminaria* growing up to the surface of the sea from a depth of 50 fathoms. Here the essential life-activities of the two plants are much the same and evolution has merely added cells to cells in such a way as to build up a plant-body which can hold on to the sea-bottom, may not be easily dislodged from its base and which can freely float in the water. Again we may compare the structurally simple fungus with a great tree, when we see that the essentially nutritive and reproductive functions are as efficiently carried on by the simple, as by the complex plant. The structural complexity of the tree is only such as is necessary for the support of a large mass of material against gravity and wind stresses, and for the conduction of water throughout all parts of this plant body. And we see also in the large, multicellular plants the surplus assimilation of material:

the tree, for example, synthesizes from CO_2 and OH_2 far more carbohydrate than is required for its reproductive activity and this surplus builds up the mechanical, supporting tree body.

Mobility has been the main feature of animal evolution. There is nothing that is physiological in nature that is not as efficiently performed by, say, the Infusorian as by the great marine or terrestrial mammals. In the evolution of the structurally complex bodies of the latter animals we see, first, mere increase in size; second, the development of bodily parts that enable the animal to move; third, the development of organs analogous to the circulatory vessels of the tree, whereby nutritive materials become distributed throughout a large body and, finally, the evolution of the means of integration that increased bodily size necessitates.

In the evolution of size the skeleton comes into existence. But in the large Algæ, which are floated in water, skeletal structures are unimportant. They become more significant structural parts in the great tree and still more important in the freely movable animal such as the whale or bird. It is curious that certain materials only have been incorporated in skeletal parts: cellulose in the plants and calcium salts in the animals. Why silicates have not been more important features of the plant and animal skeletons than they actually are, and why iron or aluminium salts have not been utilized in the animal skeletons, are curious problems.

In the evolutionary career, then, the main features have been (Fig. 41):

(1) Increase of bodily size; the skeleton;
(2) Development of bodily mobility;
(3) Development of organs of circulation;
(4) The integration of the bodily activities, and a further feature, which we shall study in the "episodes," is the appearance of mere, *unessential*, bodily, structural complexity. This we call "excess-value" of transformism (see Section 56).

104. *ON THE MAIN TYPES OF LIFE*

Neglecting, in the meantime, what we call unessential structural detail we find that the following main organic types have evolved:

i. The Thallophytes, including the Algæ, the Fungi, Diatoms,

Peridinians and Bacteria. The group is a dominant persistent and versatile one with few episodes in its history.

ii. The Bryophytes : iii. The Pteridophytes. The types are

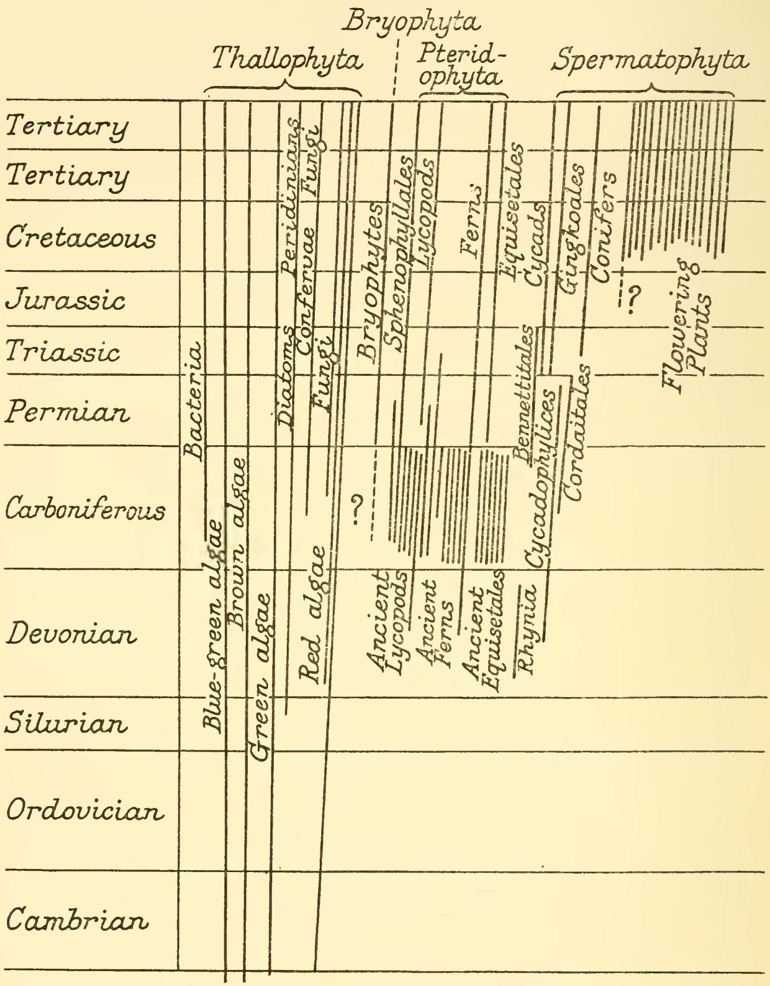


FIG. 41.—APPROXIMATE PERIODS OF THE MAIN TYPES OF PLANTS.

persistent ones, but the interest of their history lies in the extraordinary episodes of the later Paleozoic times when the Arborescent Ferns, Lycopods and Horsetails became so very abundant.

iv. The Spermatophytes. Now the dominant plants. This type was the latest of all to appear. At present it is represented by the Flowering Plants, which are certainly the most dominant and ubiquitous of all forms of terrestrial life.

v. The Protozoa. Except for such Protozoa, like the Radio-

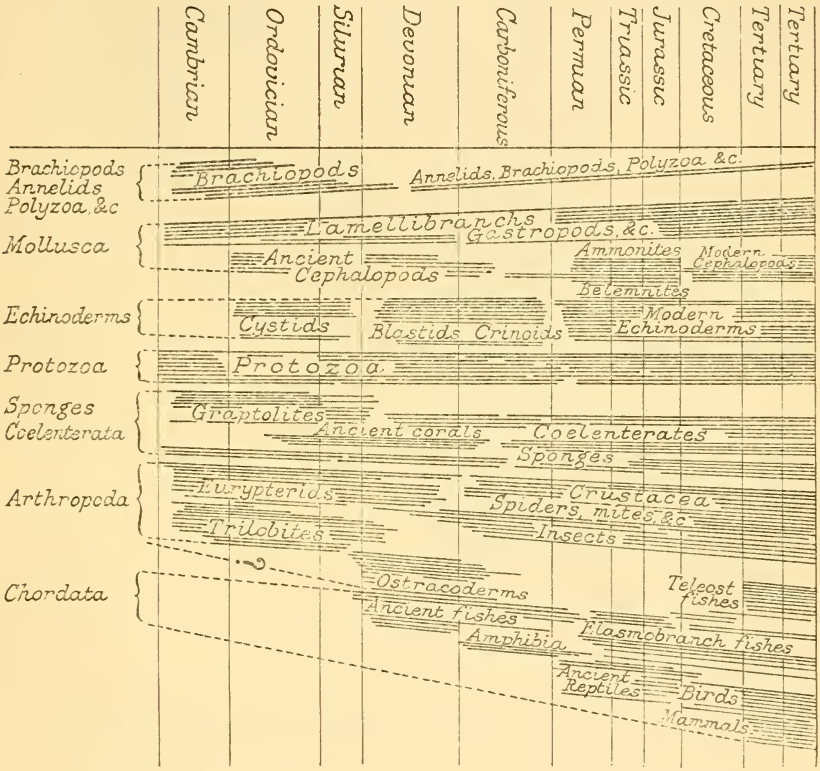


FIG. 42.—APPROXIMATE PERIODS OF THE MAIN TYPES OF ANIMALS.

laria, which have skeletons capable of fossilization, we know little of the past of these organisms. But there is little doubt that they have been a widely distributed and ancient form of life.

vi. The Sponges and Cœlenterates. Ancient and persistent forms of animals with few vicissitudes in their past history.

vii. The Molluscs, including the Lamellibranchs, Gasteropods, Cephalopods, Heteropods, etc. There have been Lamellibranchs

and Gasteropods since the earliest known times and these are the main molluscan types. They exhibit persistence and mediocrity. We shall study the episodial Cephalopods presently.

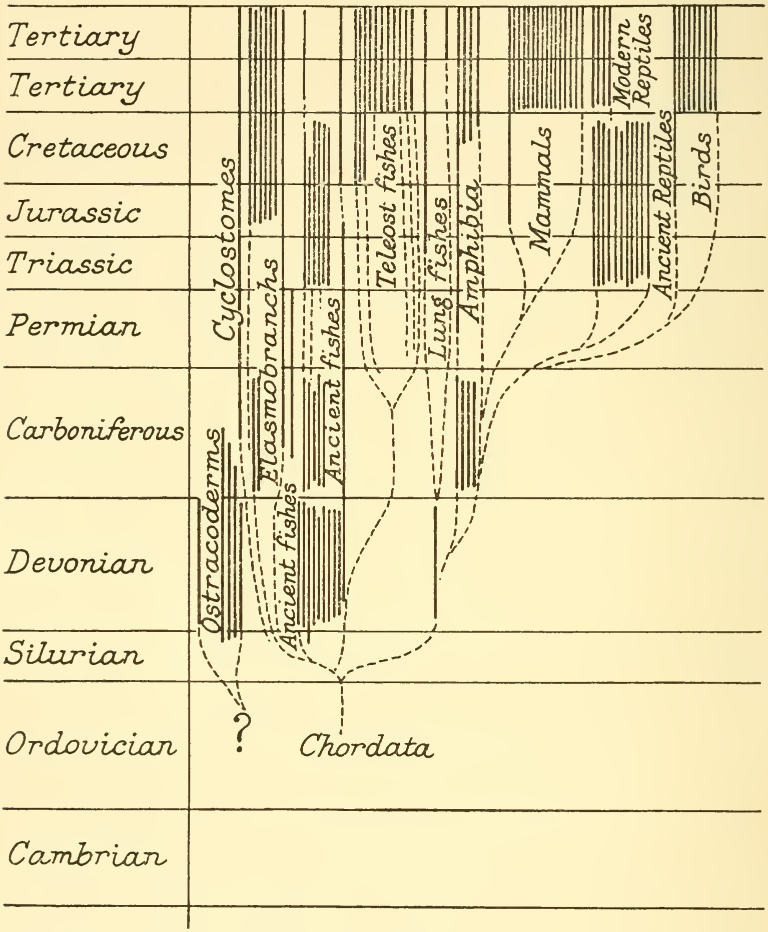


FIG. 43.—PERIODS AND AFFINITIES OF THE CHORDATE ANIMALS.
The dotted lines suggest the affinities.

viii. The Brachiopods, Polyzoa, Annelids, etc. A mixed group of animals related to each other in ways that are difficult to trace. They, also, have always been an animal type that is persistent and of mediocre density.

ix. The Echinoderms. A group of persistent and specialized animals that have displayed episodes of considerable interest.

x. The Arthropods. Perhaps the oldest known group of

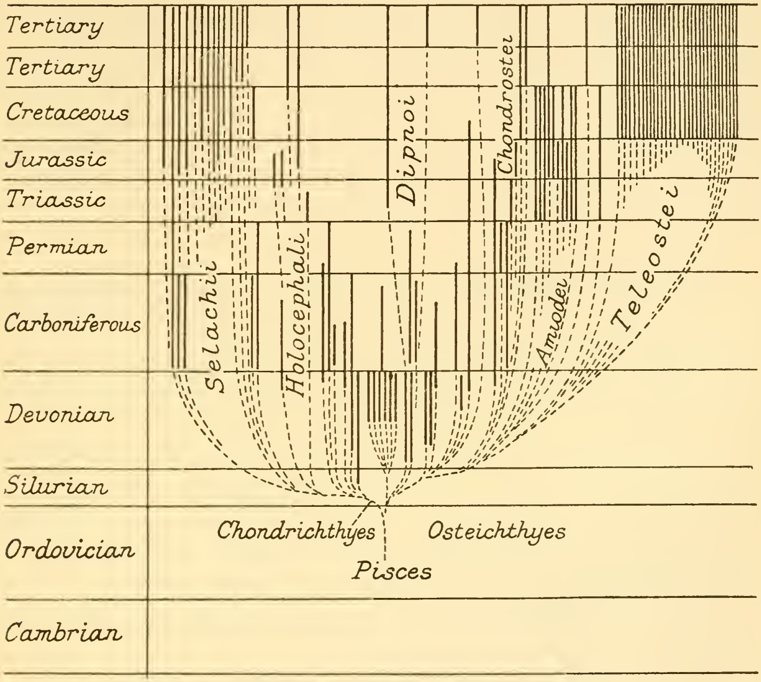


Fig. 44.—Periods of Main Groups of Fishes.
The dotted lines suggest the affinities.

multicellular higher animals. After their early episodial developments they have been a type of continually increasing dominance.

xi. The Chordates. Here we provisionally include the extinct Ostracoderms. On the whole the idea of "progress" in evolution is best illustrated by the Chordates. Fig. 43 suggests this in the way in which the various sub-groups of vertebrate animals are made to show convergence. This figure and also Fig. 44 are also attempts to make phylogenies. But it must be understood that there is hardly any warrant in the paleontological evidence for the linking together of the sub-groups, and the consequent derivations, that are suggested by the dotted lines.

These express inferences are based only on morphological resemblances and differences.

At the present time all these types of living things exist, but these categories are of particular significance :

(1) The Thallophytes and, in particular, the Algæ and Bacteria ;

(2) The Flowering Plants ;

(3) The Arthropods, particularly the Insects and Crustacea, and

(4) The Vertebrates, particularly the Teleostean Fishes and Mammals, and we may say that these are the most ubiquitous and dominant groups of living things on the earth.

105. *ON THE DEPLOYMENTS OF LIVING THINGS*

Several times during the evolutionary career there has been the sudden appearance of some type of organisms and then the rapid divergence of a number of sub-types. Such deployments have been :

i. That of the Metazoan phyla in the Cambrian and Silurian periods ;

ii. The great deployment of the Pteridophytes—that is, the arborescent Ferns, the arborescent Lycopods and Horsetails and of the Pteridosperms during the Carboniferous period ;

iii. The spread over the earth, following the Cretaceous period, of the flowering plants.

Almost at once, as it appears, such groups of organisms have evolved and become widely distributed, and there is no evidence, in any case, of origins from other organic stocks. It may be the case that the sudden deployment of the metazoan phyla at the beginning of the Paleozoic periods is illusory and that there was a long anterior process of divergent evolution that is concealed by the great destruction of fossils during the period represented by the unconformity that exists between the Paleozoic and Proterozoic strata. That unconformity may represent the destruction, by erosion, of a very great thickness of strata which may have contained transitional fossils. But there is no such extensive unconformity between the Silurian and Devonian strata and yet a similar deployment marks the first extensive land flora. Nor is there any great unconformity between the Cretaceous and Jurassic periods in which the records of the evolution of the

Flowering Plants might be lost. It cannot be said that these characteristic features of the evolutionary process are, as yet, susceptible of satisfactory descriptions.

106. *ON THE EPISODES OF LIFE EVOLUTION*

We may best present these in tabular form :

The Leading Type.	The Episodes.	The Period.
Pteridophyte .	The great tree ferns The great Lycopods The Equisitales	Carboniferous.
Cœlenterate .	The Graptolites	Cambrian to Devonian.
Brachiopod .	The old Brachiopods	Cambrian to Devonian.
Echinoderm .	Crinoids Cystids Blastids	Cambrian to Carboniferous
Mollusc . .	Ancient Tetrabranch Cephalopods	Ordovician to Carboniferous.
	Ammonites and Belemnites	Permian to Jurassic.
Arthropod .	Eurypterids Trilobites	Cambrian to Devonian.
Chordate (or Arthropod) .	Ostracoderms	Devonian to Carboniferous.
Chordate . .	Ancient fishes Ancient Amphibians	Carboniferous to Permian.
	The great Reptiles	Permian to Cretaceous.

In each episode some offshoot from the leading type has evolved and become temporarily dominant. Such phases of dominance we refer to as the " Age of Brachiopods," " Age of Trilobites," etc. The episodial group appears rather suddenly in each case, becomes established and dominant and then undergoes remarkable amplification in unessential structure. As in the cases of the Trilobites, the Mesozoic Cephalopods, the Permian, Triassic and Jurassic Reptiles, etc., there are bizarre specializations of structure. Then follows the phase of degeneracy of the episodial race and its total extinction, or loss of dominance, to be followed by the survival of only a few representatives.

The Darwinian principles of natural selection and adaptation have been employed to explain such features of the episodes. Elaboration of structure has been taken to mean greater adaptation

to natural conditions and so increased distribution and dominance. Then, it is said, " over-specialization " followed, with failure of the episodial organisms to adapt themselves to the natural conditions. But there must have been a phase in the process when satisfactory adaptation of structure (and assumed functioning) had been attained. Why, then, did the organisms continue the process of amplification to the phase when their structures had become detrimental in the struggle for existence? It would appear that some *impulse* to elaboration of structure and functioning had been the prominent and inevitable process leading to the episode.

107. *ON THE FUTURE OF THE EVOLUTIONARY CAREER*

No results of modern biology enable us to predict transformist processes. It will be seen, on sufficient reflection, that so-called Mendelian predictions of the results of breeding experiments are only statements of the probabilities of the combinations of known structural characters: they are entirely analogous to, say, the results of drawing a sample from a box in which known numbers of differently coloured balls have been mixed. The new thing in a transformist process is a mutation. Mutations appear with the semblance of spontaneity. Such changes are said to be physically " induced," say by exposing a breeding animal to X-radiation, but the nature of the change cannot be predicted. Evolution, as we have already pointed out, is essentially the appearances of *novelties* in a process, and no hypotheses yet formulated, whether these postulate the " induction," by the " environment " of mutations, or the evolution of that which is already " involved " (as in the preformation speculations), or whether they include the vague and confused notion of " emergence," can stand up to the test of prediction.

107*a*. THE TIME-SCALE AND PHYSICAL CONDITIONS. It is certain that evolution has been in operation for a period of 600 millions of years. It is probable that the physical conditions throughout that period have been much the same as they are at present and will be for some future period of the order of thousands of millions of years. It may seem quite preposterous to attempt to contemplate what will happen in the future in the light of our knowledge of the past and from what little we know as to the

physical conditions under which organisms may exist. Yet we know that life is materialized in a very few kinds of matter and we cannot anticipate any material evolution in even those thousands of millions of years that we contemplate. We know, with some confidence that geological changes, cyclical, cosmic and seasonal changes, gravity, solar radiation, temperature limits, etc., will be very much the same for thousands of millions of years to come as they were in the past history of our planet. And that being so we cannot anticipate any radical changes in the life that exists on the earth.

For even the 600 millions of years that have elapsed since the Cambrian deployment are a significant fraction of the total evolutionary period that we envisage. In that time about a dozen great types of living things have evolved—*and having once evolved they have persisted.* No new phylum has come into existence and no phylum has suffered extinction. The vicissitudes of evolution have been expressed only as the episodes and these we may regard as non-essential structural and functional developments that represent what we have called excess-value in transformism. They have not been, like the great phyla, persistent and successful processes. They are simply what we have called them, episodes in a main theme that continues. It may not be at all foolish to maintain that already the full possibilities of the materialization of life on the earth have been realized.

107*b*. MAN. But it is not certain that we should regard the evolution of man as only an episode. We might take that view if we were to restrict our speculations to man, the mammal, and refuse to consider man *as himself a transformist agency*. As an animal we should have no reason for thinking that man is not exposed to all the risks that other highly specialized animals have endured in the past. We should not have any confidence, for instance, in supposing that man, the Mammal, may always retain dominance over the equally ubiquitous and formidable insects.

But we do not seem obliged to impose any limits (other than those inherent in the passage of nature) on man's power of influencing the changes that proceed on the earth: we have seen, for instance, that even now man can affect (infinitesimally, that is) the course of evolution of the bodies in the solar system. We know that during the very short period of a few thousands of

years man has, very sensibly, influenced the distribution of forms of life on the earth ; that he has caused the appearance of many new kinds of useful plants and animals, has eliminated other species and that it is certain he will do so, in his own interests, in an increasing degree in the future. We may place no immediate limits on his power over nature. Even should human mentality not evolve further than it has done, the progress of scientific knowledge in the past assures us of the expectation of further progress in the future. We may be certain that anything that can be clearly thought out (as a train of mathematical reasoning is thought out) is ultimately susceptible of " physical significance," that is, may ultimately resolve itself into power over nature. We may not, then, regard human evolution merely as an episode in the vertebrate type of organisms, for man *may* become sensible of whatever excess-value his own evolution implies and will acquire the power of averting his own loss of dominance as an animal.

That does not mean that human civilization, as we know it, may not be an episode. This civilization of the present does, indeed, present no element of persistence. Clearly it expresses itself in forms that are based on the exploitation of natural energy-accumulations (coal and oil) that are unrenewable in those periods of time by which we measure the durations of civilizations. Just as clearly our present civilization will undergo extinction within the few centuries, or at most thousands of years, that measure the practical exhaustion of those natural energy-stores. In spite of all that has become known as to the almost immeasurable quantities of energy that exist in the bound mode (in the atoms) we cannot envisage any immediate possibility of bringing that energy under human control. It may be that such processes as those of the " annihilation of matter " and the consequent release of free energy can proceed only under conditions that make the materialization of life impossible (that is in such physical states as we imagine in the interiors of the stars) and it may be that the radio-active disintegrations of the atoms are phases in the passage of nature that are already " made " (Section *2e*) and which we cannot influence. In such a cosmic process it would appear that human civilizations must revert to the persistent pastoral-agricultural type. Of course what we do know of the physical conditions that we call " transcendental " expresses our

present knowledge only. It can be argued that what we call our "knowledge" is rather to be regarded as our power of control of natural events. ("In the Beginning was the Act," and thought came after action.) Therefore it may be that we do not, as scientists, search for "absolute truth" but really for power. And so the limitations that we have suggested above may not exist, and since there is mental evolution the barriers that cosmic processes impose upon our power may be illusory ones.

Still we have to think, just yet at all events, of Man, the Mammal. As such we have inherited modes of mentality, acquisitiveness, the predatory instinct, etc. How very strong these inherited modes of action are the history of the scientific-industrial-capitalistic civilization shows us. The argument against a communal civilization that both its protagonists and anatagonists recognize is the improbability that men will "do their best" for any other than individualistic motives. Individual motive, we see clearly, is very powerful in the building of civilizations. We do not deal only with the primary urges that are active in the origin and maintenance of gregariousness but also with the impulses of greed, acquisition and the lust for power and here we can see clearly the ways in which civilizations based on the acquirement of unlimited energy may be wrecked. So the evolutionary history of the earth during the next thousands of millions of years may still be that of man, the dominant animal, but also that of civilizations that are episodial, self-destructive and recurrent.

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